Investigating the habitat selection and dietary preferences of a largely sedentary population of blue wildebeest in the Kgalagadi Transfrontier Park – impacts of permanent surface water provision in a semi-arid environment.

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Photo credit: Shane Muhl

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Abstract

The continued provision of waterholes since the early 1930s has facilitated the formation of a largely sedentary population of blue wildebeest (*Connochaetes taurinus*) in the Kgalagadi Transfrontier Park. However, other environmental variables may influence the distribution of this resident herd within the riverbeds of the Park. I explore the effects of water quality, forage abundance, tree density and river width on wildebeest habitat selection. I do this through a combination of an analysis of two years of wildebeest census data, published water quality data and a series of transects across the Auob and Nossob rivers for dung and grass sampling in the Park. My results show that water quality is a key predictor of wildebeest distribution, with animals strongly selecting for areas with access to fresh water over areas with saline or no water. Shade also emerged as a strong predictor of wildebeest distribution, demonstrating the importance of thermoregulatory behavioural adaptations in this arid savannah system. Wildebeest avoided areas of the riverbed that were densely vegetated, instead showing a preference for wider, open areas. This preference is likely a combination of two factors; enhanced predator detectability in open regions of the riverbed and the larger area of short grass communities present in this habitat.

In this arid environment the distribution of available graze has long been considered an important variable in determining the distribution of wildebeest. I further examine my results showing that forage availability and quality plays a key role in wildebeest habitat selection through a stable carbon and nitrogen isotope analysis of wildebeest dung and the leaves of common shrubs and grasses to explore the spatial and temporal variation in wildebeest diet. These results show that wildebeest in my study site consumed a higher proportion of C_3 plants than previously recorded in other areas of their range. This C_3 intake increases in the dry season and in marginal, low use areas of the Park, suggesting that C_3 plants are an important alternative food source to wildebeest during drought periods. This increase in C_3 plants allow the animals to maintain their crude protein requirements throughout the dry season, despite a pronounced drop in the quality of available graze during this period. These results suggest that wildebeest were not food limited during the study period, although the distribution of these animals appears to largely reflect bottom up (resource based) mechanisms.

A portion of the resident herd displayed some level of local movement, dispersing out of the riverbeds during the wet season before concentrating again near good quality waterholes in the dry season. This movement is likely driven by increased wet season forage outside the riverbed habitat and facilitated by ephemeral pools of water that form in pans in the rainy season.

Grass species counts and grazing evidence were used to investigate the grazing habits of all herbivores in the riverbeds of the KTP. My results suggest that herbivores are more restricted in their grazing choices during the dry season. While there was no conclusive evidence to suggest that this was a direct result of grass quality, it is likely that the pronounced decrease in grass quality during the drier months does play a role in herbivore grazing habits.

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CHAPTER 1

1.1 Introduction

The Kalahari is an arid savannah stretching over more than 2.5 million km^2 of southern Africa. Covering much of the southern region of the Kalahari is the largest conservation area in the broader Kalahari System the Kgalagadi Transfrontier Park (KTP) (SANParks 2008). Historically this area consisted of two parks; the Kalahari Gemsbok National Park of South Africa and the Gemsbok National Park of Botswana, before officially uniting as the Kgalagadi Transfrontier Park in 1999 (Mills & Haagner 1989; Stapelberg 2007). The Nossob River acts as a natural boundary between these historical parks and today forms the border between South Africa and Botswana. The Park is fenced off along the Namibian/South African border to the west but remains open all the way to the Central Kalahari Game Reserve to the east (Thomson & Shaw 1991; SANParks 2008).

Despite the arid climate many of the topographical features in the Kalahari have been shaped by water with the park divided into central and southern drainage regions by the Bakalahari Schwelle divide (Thomson & Shaw 1991). The ephemeral Okwa River drains the central Kalahari northwards while the southern Kalahari is drained by four ephemeral rivers, the Kuruman, Molopo, Auob and Nossob, all meandering south to join the Orange River that flows west to the Atlantic Ocean (Knight 1991). In the KTP the Auob and Nossob riverbeds form shallow river valleys that remain dry and only flow for short periods during exceptionally wet years (Steenkamp *et al*. 2008). There is no naturally occurring surface water in the Park and pools that form after wet season rains rapidly evaporate in the intense heat (de Vries *et al*. 2000). Groundwater however is plentiful throughout the Kalahari region and deep aquifers located below the underlying Karoo basalt are a source of water for deep rooted tree species as well as for the many waterholes in the Park (Canadell *et al.* 1996; Thomas & Shaw 1991; Shadwell *et al.* 2017).

In the 1930s shortly after the formation of the Kalahari Gemsbok Park the authorities sunk a series of waterholes in the dry riverbeds of the Auob and Nossob rivers. Since then artificially provisioned surface water has been an integral part of the KTP (Knight 1991). These waterholes were initially established to provide water to migratory species during the long dry season and to maximize the tourist potential of the Park by attracting animals (Child *et al*. 1971; Van Wyk & Le Riche 1984). The provision of surface water has however since been

questioned, with concerns arising over the consequences of this management technique (Bothma & Mills 1977; Eloff 1959; Eloff 1962, Owen-Smith 1996). Permanent surface water provision in arid systems can influence the distribution and behaviour of herbivores (Brits *et al*. 2002; Gaylard *et al.* 2003), which includes their seasonal range and habitat preference across the landscape. These changes can thus significantly alter the extent and timing of defoliation pressure on associated plant communities, causing shifts in vegetation community composition and structure (Augustine & McNaughton 1998; Bråthen *et al. 2007*; Plas *et al.* 2016).

The blue or common wildebeest (*Connochaetes taurinus)* is a large herbivore that occurs in savannah ecosystems in southern and East Africa (Kingdom *et al.* 2013). Although resident populations do form, wildebeest are particularly well known for the vast migrations they undertake in parts of their range, most notably in the Serengeti (Bell 1971; Holdo *et al.* 2009). Migrating wildebeest will typically move to areas with high quality forage during the wet season, and return to areas with higher forage quantities but lower quality during the dry season (Holdo et al. 2009). These migrations are thus primarily driven by forage quantity and quality, which are in turn determined by a combination of rainfall and soil nutrients (Bell 1982). However, wildebeest are a water-dependent species (Western 1975), and so herd distributions in relation to forage resources are necessarily constrained by the availability of drinking water. In some areas wildebeest migrations have been severely disrupted by human activity. The construction of fences that prevent animals from accessing different seasonal foraging areas has led to large declines in wildebeest populations, e.g. in southern Botswana (Spinage 1992) and in South Africa (Whyte & Joubert 1988).

The historical movement of wildebeest in the southern Kalahari can be described as sporadic wet season dispersal (Child *et al*. 1971; Mills & Retief 1984). Historically, small groups of wildebeest from the large central Kalahari population moved to drier areas in the south-west during the wet season, returning north east as the dry season approached (Skead 1980; Williamson *et al*. 1988). When waterholes were sunk along the Auob and Nossob rivers in the 1930s wildebeest began to form small sedentary populations in the Park, particularly around waterholes with low salinity levels at Mata Mata and Twee Rivieren (Eloff 1966; Child 1971; Knight 1991). The number of sedentary wildebeest in the Park continued to grow as more waterholes were sunk in 1972 (Bothma & Mills 1977) and by the mid-1970s a

sedentary population of around 400 animals had formed (Bothma & Mills 1977; Mills & Retief 1984a).

Access to water has therefore facilitated the formation of a sedentary population of wildebeest in the dry beds of the Auob and Nossob rivers (Bothma 1972; Mills & Retief 1984a; Mills & Retief 1984b). However, the fine-grained distribution of wildebeest in the KTP is likely to be influenced by the distribution of waterholes along the riverbeds, and also the quality of the water they provide. Water quality is important for wildebeest as they do not have a high tolerance for saline water (Knight *et al*. 1988; Wolanski & Gereta 2001). Other important environmental variables shaping wildebeest distributions in the KTP could include forage quantity and quality, shade availability and predation risk. Wildebeest might also show seasonal variation in their distribution within the KTP riverbeds, and may also make greater use of the areas outside of the riverbeds at certain times of the year.Shade availability can also play a part in wildebeest distribution as these animals often spend the hottest part of the day resting under shade (Ben-Shahar & Fairell 1987;Knight 1991).The density of shade-providing trees may therefore play a role in wildebeest habitat selection, particularly in a semi-arid savannah system such as the southern Kgalagadi where daily warm season temperatures often exceed 40°C (Mills and Retief 1984). Predators may also influence the distribution of herbivores not only through direct predation, but also through indirect behavioural changed (Laundre et al. 2001). For example enclosed areas of dense vegetation that offer good cover for predators may be avoided be herbivores, restricting them to expansive open areas where visibility is high (Laundre et al. 2001; Riginos 2015). Vegetation structure can therefore govern habitat preference of savannah herbivores through the effect it has on visibility.

Rainfall is the main determinant of forage quality and quantity in this semi-arid environment (van Rooyen *et al.* 1984, van Rooyen 1990). The highly seasonal and spatially sporadic rainfall patterns in the KTP are thus likely to influence the quality and quantity of grasses (van Rooyen & van Rooyen 1998), leading to spatial and temporal fluctuations in the suitability of the primary food source of wildebeest (Knight 1991; Owen-Smith 1982). Forage attributes may therefore influence the distribution of the sedentary population of wildebeest in the KTP to some extent. Wildebeest are known to graze predominantly on C_4 grasses throughout the year, particularly in the northern and north-eastern parts of their range (e.g. Tieszen *et al.* 1979; Owen-Smith 1982; Gagnon & Chew 2000; Cerling *et al*. 2003).

Some populations do however supplement their diet with C_3 browse when grass availability or quality decreases (van Zyl 1965; Skinner & Smithers 1990) Wildebeest were also historically absent from the KTP during the dry season, and it is therefore important to establish what components of the vegetation form the basis of the diet of a resident population during this period. This will likely have repercussions both for the general health and long term demography of this sedentary population, and may also have important consequences for vegetation communities in the KTP. (Brits *et al*. 2002).

In this thesis I investigate the drivers of fine-grained wildebeest distribution in the KTP. Chapter 2 is a detailed description of my study site; the local climate, geology and the flora and fauna in the Park. In Chapter 3 I look at park-level drivers of wildebeest distribution using monthly animal surveys together with environmental variables measured in the field as well as climate and remote sensing data.

In Chapter 4 I explore the feeding ecology of wildebeest to understand which vegetation communities they rely on and subsequently which are most likely to be impacted. To do this I use stable carbon and nitrogen isotope ratios of the leaves of common shrubs and grasses as well as wildebeest dung to investigate the seasonal and regional variations in wildebeest diet (Codron *et al. 2007;* February *et al.* 2017).

My study concludes with a brief summary of my findings in Chapter 5.

CHAPTER 2

Description of the study area

2.1 Study Site

My study site is along the Auob and Nossob rivers located in the 9710 km^2 South African section of the KTP.

2.2 Climate

Mean annual rainfall for the region is 196 mm in the north (Nossob), 177 mm west (Mata Mata) and 209 mm in the south (Twee Rivieren) (Fig. 1.1), and is distinctly seasonal with 90% of annual precipitation in the hot season from January to April (van Rooyen *et al*. 1990; Tyson 1986). Inter-annual rainfall variability over a 30 year period is high throughout the KTP (CV rainfall: Twee Rivieren = 36%, Mata Mata = 52% and Nossob = 44%) (SAWS 2016). Rainfall during the 26-month census period (see below) was close to the long term average, but conditions were drier during the vegetation sampling for my study (Fig. 1.1).

During the warmer months (September through to April) maximum day time temperatures range between 30°C and 40°C, while the cooler months (May through to August) experience much colder day time maximas between 17°C and 25°C (Mills and Retief 1984; van Rooyen *et al*. 1990). Night time temperatures may drop to -10°C in the cooler months (July – August).

2.3 Geology

The drier southern region of the Kalahari is characterized by aeolian sands forming parallel dunes and sandy depressions. These soils are low in nitrogen (NH_4^+ = 5.1±1.3 mgN100g^{-1}), and phosphorous ($PO_4^{3-} - P = 1.2 \pm 0.3$ mgP100g^{-1}) (Knight 1999; Dougill & Thomas 2004). In the pans and riverbeds, fine soils (< 90% sand) accumulated by water activity dominate. These soils are more nutrient rich, containing minerals and clay that are absent in the aeolian sands and do not hold moisture well, encouraging run-off and evaporation (Thomson and Shaw 1991; van Rooyen and van Rooyen 1998).

Along the Auob and towards the southern reaches of the Nossob rivers the calcrete sheet that underlies much of the Kalahari is evident (Child, Paris & Le Riche 1971). In some areas this has led to the formation of calcic horizons, such as those found in pans and drainages (van Rooyen 1984; Stapelberg 2007).

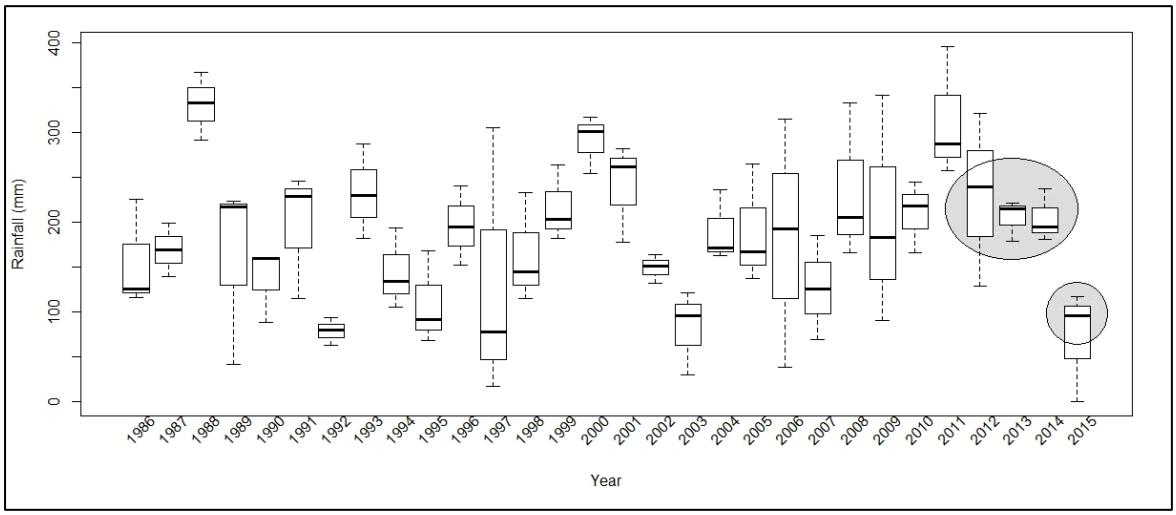

Fig. 1.1. *Average annual rainfall for Mata Mata, Twee Rivieren and Nossob camps (1985 to 2015, data obtained from SAWS 2016). Shaded areas denote periods during the study for SANParks census data counts (2012-2014) and field work (2015). The line in each of the boxes represents the median while the lower and upper limits are the 75th and 25th percentiles. The dotted lines show the non-outlier range.*

2.4 Topography and regional classification

The Auob and Nossob rivers are the dominant topographical features of the southern KTP, cutting through the dunes southwards and converging just north of the tourist camp at Twee Rivieren (Fig. 1.2). These rivers only flow episodically after periods of unusually high rainfall but are important because of the deep aquifers that have formed beneath them (Shadwell & February, 2017). The higher nutrient and water availability in the riverbed habitat support a greater diversity of grass species and more trees than the surrounding dune environment (van Rooyen & van Rooyen 1998), providing food and shade for many of the regions herbivore species (Milton & Dean 1995; Shadwell & February 2017).

I divided the study site into three regions based on broad differences in the vegetation, geology and width of the Auob and Nossob rivers (Fig. 1.2). These three regions are the northern and southern Nosssob regions and the Auob region.

The boundaries and riverbed lengths of the three regions used in my analysis (Fig. 1.2) are as follows:

- Northern Nossob: 176.5 km (starting 15 km south of Nossob camp and ending at Unions End).
    - GPS co-ordinates: S 25° 33' 24.7" , E 20° 40' 21.9" to
      S 24° 45' 41.6" , E 19° 59' 49.7"
- Southern Nossob: 128.5 km (starting at Twee Rivieren and ending 15 km south of Nossob camp).
    - GPS co-ordinates: S 26° 26' 6.7" , E 20° 37' 36.5" to
      S 25° 33' 24.7" , E 20° 40' 21.9" .
- Auob : 115 km (the Auob riverbed; starting at Mata Mata and ending at Twee Rivieren).
    - GPS co-ordinates: S 25° 45' 44.1" , E 19° 59' 44.5" to
      S 26° 26' 6.7" , E 20° 37' 36.5" .

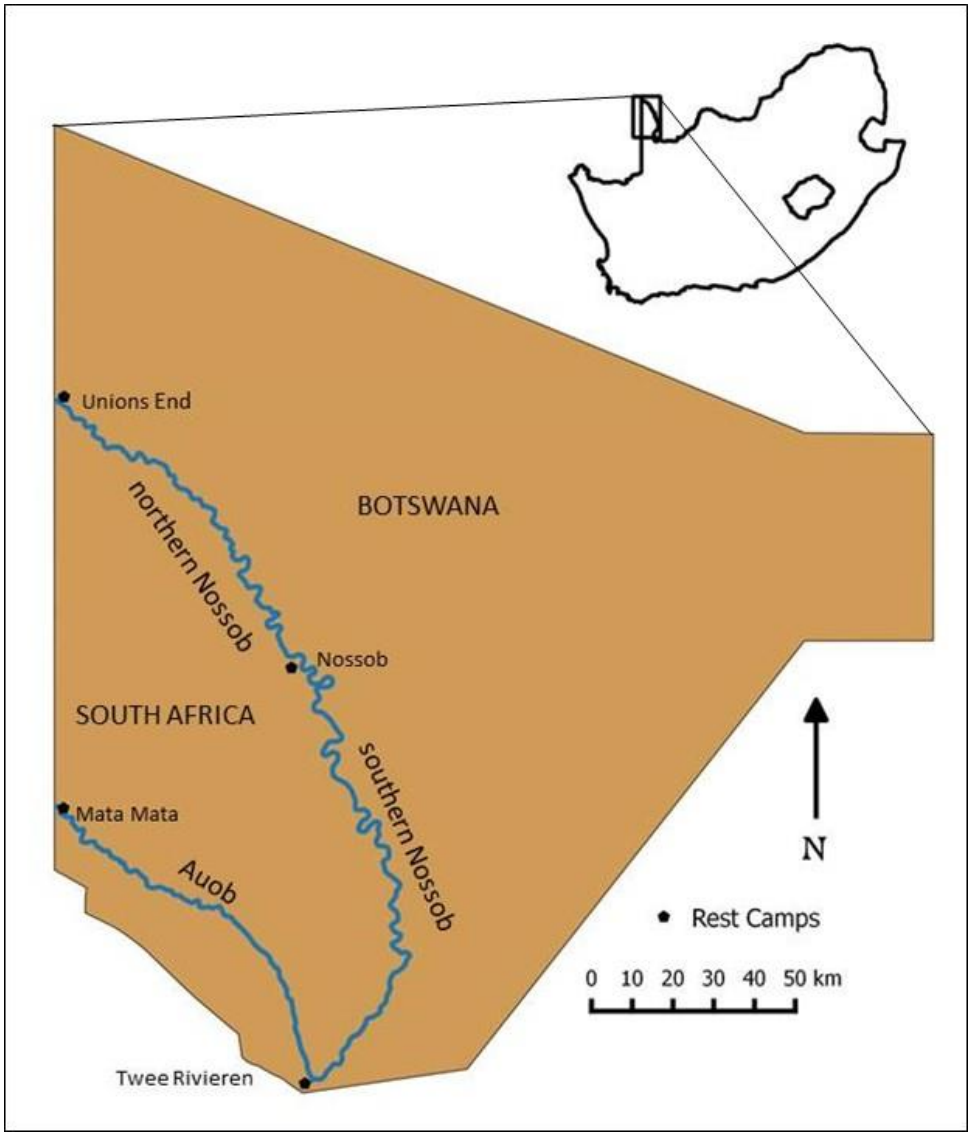

Fig. 1.2. *The study area showing the location of the three regions (Auob, southern Nossob and northern Nossob) used in this study.*

The widest section of riverbed is in the northern Nossob region, between Unions End and Nossob Camp, with an average width of about 400 m, although this can stretch to as wide as 700 m (e.g. near Rooikop waterhole; -25° 27' 6" S, 20° 36' 55.08" E). The vegetation in this section of the riverbed is sparse with no shrub cover, and the river has low sandy banks (van Rooyen *et al*. 2008). The southern Nossob region extends south from the Nossob Camp to the park's southern boundary at Twee Rivieren. The riverbed is narrow in this region, with an average width of about 200 m. The vegetation in this region is characterized by *Galenia*

africana var. africana shrubs, at times growing in dense clumps in the riverbed (van Rooyen *et al*. 2008). The riverbanks of the southern Nossob region are steep and often adorned with white calcrete clumps exposed by erosion. The Auob River in the west forms the third study region. Here, the Auob riverbed is narrow, with an average width of about 150 m. There is less shrub cover than in the southern Nossob region, although patches of *Galenia africana var. africana* are still relatively common, especially in the south near Twee Rivieren (van Rooyen *et al*. 2008). The banks are steep and often have exposed calcrete outcrops both at the top and in the middle of the bank profile.

2.5 Water availability and quality

There are a total of 42 waterholes located in the Auob and Nossob rivers; 17 in the Auob, 10 in the southern Nossob and 15 in the northern Nossob (Mills & Retief 1984). The density of these waterholes decreases from the Auob (6.8 km/waterhole) through the southern Nossob (11.8 km/waterhole) to the northern Nossob (12.8 km/waterhole). Dreyer (1987) used percentage salinity as a measure of water quality with salinity concentrations below 3% to denote fresh water. He found that only three waterholes in the Auob have a salinity percentage > 3%, while in the Nossob he only found waterholes with a salinity percentage ≤ 3% close to Twee Rivieren in the south and around Nossob and Unions End camps in the north (Dreyer 1987).

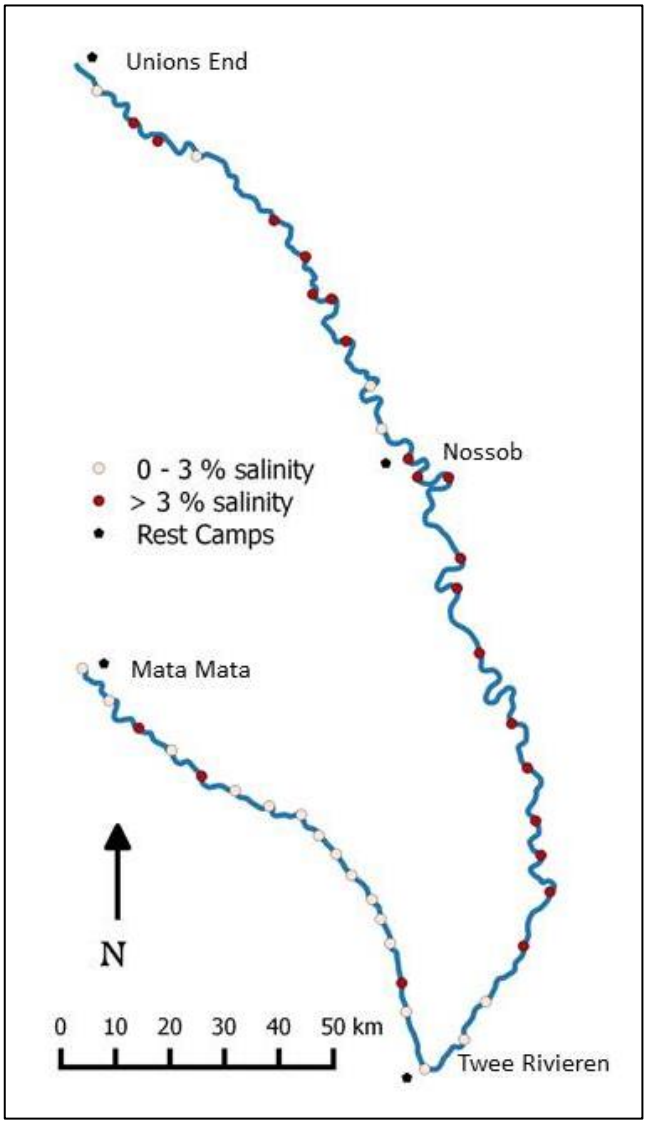

Fig. 1.3. *Salinity (%) as a measure of water quality from Dreyer (1987). No data were available for three of the 42 waterholes (Nossob, Polentswa and Geinab). These three waterholes are all located in the northern Nossob.*

2.6 Vegetation

The vegetation at my study site has been classified into seven distinct categories (van Rooyen 2000; van Rooyen et al. 2001; Stapelberg 2007);

1. Dune crests are characterized by predominantly red, loose and coarse Aeolian sand. Tall grass species such as *Stipagrostis amabilis* and *Eragrostis trichophora* are common. Woody species include *Acacia haematoxylon, Acacia mellifera, Acacia erioloba,* and *Boscia albitrunca.*
2. Grassy plains characterize much of the interior dune landscape. These areas of deep red sand and undulating low dunes have grass species such as *Centropodia glauca, Stipagrostis uniplumis, Eragrostis lehmanniana* and *Schmidtia kalihariensis.* Woody plant species include *Acacia haematoxylon* and *Grewia flava.*
3. Communities of the low dunes and plains represent typical open to dense tree savannah, characterized by woody species such as *Acacia erioloba, Acacia luederitzii* and *Boscia albitrunca.* The shrub *Acacia mellifera* is also evident, along with dwarf shrubs such as *Rhigozum trichotomum* and *Asparagus nelsii.* Grass species include *Centropodia glouca* and *Schmidtia kalihariensis.*
4. The edges of rivers and pans, as well as dune valleys, are characterized by compact sands that range in colour from pink to white. Shrub species such as *Rhigozum trichotomum* and *Monechma incanum* create a typical shrub savannah, with common grasses *Stipagrostis obtusa, Schmidtia kalihariensis* and *Stipagrostis ciliata.*
5. Calcrete outcrops are most commonly encountered on the southern banks of the Nossob and throughout the Auob. The grass layer is poorly developed, although *Stipagrostis obtusa, Stipagrostis ciliata* and *Enneapogon desvauxii* are often evident. Woody species include *Acacia erioloba* and *Boscia albitrunca,* as well as shrubs such as *Rhigozum trichotomum* and *Monechma incanum.*
6. White, clayey, calcareous soils make up the numerous pans within the region. Grasses such as *Enneapogon desvauxiia, Tragus racemosa,* and *Eragrostis annulata,* as well as shrubs such as *Lycium cinereum, Monechma incanum* and *M, genistifolium* dominate.
7. Plant communities found in the Auob and Nossob Riverbeds grow on silty, clayey soils of alluvial origin. Grasses are predominantly annual such as *Enneapogon desvauxiia, Tragus racemosa,* and *Chloris virgata* dominate, but perennial species such as *Panicum coloratum, Eragrostis rotifer* and *Stipagrostis obtusa* are also

common. Large *Acacia erioloba* and *Acacia haematoxylon* are scattered within the riverbeds, and much of the area is dominated by the unpalatable shrub *Galenia africana* var. *africana.*

2.7 Fauna

The southern Kalahari has a wide range of animal diversity with 60 mammal species, 300 species of bird, and over 55 species of reptile in the South African section of the KTP alone (van Rooyen 2000).The dominant species of indigenous antelope include the blue wildebeest (*Connochaetes taurinus taurinus),* gemsbok *Oryx (gazella gazelle),* eland (*Tragelaphus oryx),* grey duiker (*Sylvicapra grimmia),* red hartebeest (*Alcelaphus buselaphus buselaphus),* springbok (*Antidorcas marsupialis),* and steenbok (*Raphicerus campestris;* Stapelberg 2007). The region is also home to a number of predators; lion (*Panthera leo),* leopard (*Panthera pardus),* cheetah (*Acinonyx jubatus),* spotted hyaena (*Crocuta crocuta)* and brown hyena (*Hyaena brunnea)* occur throughout the KTP.

CHAPTER 3

Spatial and temporal distribution of wildebeest in the Auob and Nossob riverbeds.

3.1 Introduction

Large herds of wildebeest are known to move long distances in search of better quality forage and surface water, exploiting temporal and spatial variation in foraging conditions and surface water availability (Holdo *et al*. 2009). Groups of blue wildebeest historically migrated into the southern Kalahari from the Central Kalahari in the wet season, before returning northwards at the onset of the dry season (Eloff 1961, Williamson *et al*. 1988). The introduction of permanent waterholes in the Auob and Nossob riverbeds has disrupted this migration pattern, and resulted in the establishment of a sedentary population of wildebeest in the KTP (Bothma 1972; Mills & Retief 1984; Mills & Retief 1984b). However, while the reliable availability of drinking water allows wildebeest to persist year-round in the KTP, the relative importance of surface water and other environmental variables as determinants of wildebeest distribution is not well understood.

Wildebeest are a water-dependent species (Western 1975), preferentially making use of drinking water with low concentrations of total dissolved solids and low salinity (Parry 1987; Knight *et al*. 1988; Skinner & Smithers 1990). For example, in the Amboseli ecosystem, 90% of wildebeest were found to occupy areas within 4 km of water during the dry season (Western 1975), and higher densities of wildebeest were recorded within 3 km of water in the Kruger National Park (Smit *et al.* 2007). Previous work in the KTP has also shown that boreholes with less saline water are strongly correlated with the establishment of sedentary wildebeest populations in different regions of the Auob and Nossob rivers (Eloff, 1966; Dreyer 1987; Bothma 1972; Bothma & Mills 1977). The distribution of wildebeest in the KTP should therefore be closely linked to the availability and quality of surface water (Child *et al*. 1971; Williamson *et al*. 1988).

Although access to water is an important factor shaping wildebeest distributions, vegetation structure is also important for determining which areas they utilise (Smit & Grant 2009). Wildebeest are classified as obligate grazers with graminoid species making up >90% of their diet (Owen-Smith 1982; Gagnon & Chew 2000; Codron *et al*. 2007). As in many other arid

savannah systems, the availability of these forage requirements will vary in response to sporadic and spatially variable thunderstorms that determine landscape level variation in productivity (Frank *et al.* 1998; Augustine *et al.* 2003). Spatio-temporal variation in forage quality and quantity should also determine the distribution of wildebeest in the KTP (Grant & Scholes 2006; Augustine *et al.* 2003). Wildebeest often spend large parts of the day resting and ruminating (Ben-Shahar & Fairall 1987), and their diurnal activity decreases with increasing temperatures (Shrestha *et al.* 2014). In a hot, arid environment such as the KTP, the availability of shade is therefore likely to be an important determinant of wildebeest distribution (Knight 1991). Tree density may thus be a useful predictor of which riverbed areas wildebeest are more likely to utilise.

While the provision of surface water has led to the establishment of a sedentary wildebeest population in the Auob and Nossob riverbeds (Mills & Retief 1984; Mills & Retief 1984b), there is still potential for wildebeest to undertake more localised, seasonal movements depending on available forage and distance to water. Such localised movement may correspond with the historical wet season influx of animals from the central Kalahari (Bothma 1977). This potential for localised movement does not however detract from the effect that sedentary wildebeest populations now exert on vegetation in the KTP with the potential for greater defoliation pressure to occur in the dry season when wildebeest historically would have been absent from the area.

Predators may also influence the distribution of wildebeest within the KTP by causing them to avoid areas perceived to be high risk, thus restricting grazing to expansive open areas, where visibility is high (Laundre *et al*. 2001; Riginos 2015). Some regions of the riverbed are wide and barren whilst other regions are narrow with dense shrub cover (van Rooyen *et al*. 2008; personal observations). River width may thus form a good proxy measure for predator visibility. The section of the Nossob River north of Nossob camp is wider and more sparsely vegetated than other regions of the study site, which I predict would make it the region where predators are most easily detected with resulting higher wildebeest numbers.

While the availability of permanent drinking water has been shown to allow wildebeest to remain in the KTP year-round (Bothma 1972; Mills & Retief 1984a; Mills & Retief 1984b), my primary objective in this chapter is to understand the relative importance of water

availability and salinity in combination with the effects of foraging conditions, seasonal timing and predation risk in determining the distribution of wildebeest within the KTP.

3.2 Methods

3.2.1 Census counts

South African National Parks made monthly surveys of the two river systems from February 2012 to March 2014 (SANParks unpublished data). For these surveys a fixed route along the Auob and Nossob rivers was driven at the end of each month, with the species number and GPS location for all large mammal sightings being recorded.

To analyse these census data, I divided the full length of the Auob and Nossob rivers into 85 contiguous 5 x 0.9 km sampling blocks. A block length of 5km was selected to arbitrarily divide the study area into comparable units and ensure a statistically viable number of blocks for each region. This block size was adequate to capture sufficient variation in wildebeest numbers and also allow for fine-scale habitat description relative to the spacing of waterholes within the riverbeds. Block width was set at 0.9 km throughout the study site to include the riverbed at its widest point. Total wildebeest counts for each block were then summed for each month of the 26-month study period.

3.2.2 Environmental variables

Forage availability

NDVI measurements do not differentiate between grass and trees but give a single measure of photosynthetic activity based on the amount of absorbed and reflected light (Gamon et al., 1995). At my study site, where trees are scattered throughout the riverbeds, this may lead to a 'tree effect', where a portion of the productivity relating to grass growth is lost due to the effect of trees on NDVI measurements. As tree density varies among plots, this amount of unavailable productivity may also vary, potentially introducing a bias. As trees are not deciduous and grass growth is highly seasonal and fluctuates dramatically over short temporal scales, I hypothesis that changes in NDVI values in space and time between plots is attributed to changes in grass biomass. I examined this by determining the relationship between the number of trees in each block and NDVI.

Normalized difference vegetation index (NDVI) data were obtained from the MODIS Terra satellite database (Didan 2015; NASA 2015). The data were obtained as 16-day composites at 250 m resolution. Monthly NDVI averages were then calculated for each block in the study area using QGIS software (Quantum GIS Development Team 2016).

These NDVI data capture the effect of rainfall on the spatio-temporal variation of forage availability. Remote sensing imagery provides a more direct measure of plant growth than rainfall, and also represents the spatial variation in forage biomass more accurately than an interpolated rainfall layer, particularly given the scarcity of rain gauges (four) in the area.

Water status

Water hole locations in the riverbeds of both the Auob and the Nossob were obtained from Robin Peterson of SANParks and verified in the field. Waterholes not in use or undergoing repairs during the census data collection were noted. None of the functioning waterholes included in the analysis were out of operation for more than two months throughout the census data collection period (John Bezuidenhout pers.com). Water quality data were obtained from Dreyer (1987) and used to classify each of the 85 study blocks into one of three water status categories: 1) 'None', if no waterhole was present in the block, 2) 'Salty' if a waterhole was present in the block but salinity exceeded 3%, and 3) 'Fresh' if a waterhole was present in the block and salinity was below 3%.

Shade availability

The availability of shade within a block was estimated by counting the number of trees with canopies greater than 1.5 m in each block using Google Earth imagery and QGIS software. These counts were ground truthed in the field by direct counts of the number of trees in six blocks (two in the Auob and four in the Nossob). These blocks were selected based on proximity to field camps and study blocks. Remotely counted trees were shown to account for 93% of the ground truthed tree counts. Trees growing on the banks of the northern Nossob or the steep stony banks of the Auob rarely showed any evidence of ungulates (sightings, dung or spoor) and counts were therefore restricted to the riverbed. Tree counts were converted to tree densities (trees/km^2) by dividing by the area of the block.

Predator visibility

Predator visibility was estimated using measurements of riverbed width. The riverbed was defined as that section of the river stretching from the mid slope of one bank to the mid slope of the opposite bank. River width was then determined using Google Earth and QGIS software. Three measurements each spaced approximately 1.7 km apart, were made for each block at my study site. These measurements were then averaged for each block.

Season

As rainfall at my study site is extremely variable average daily maximum temperatures were obtained from the South African Weather Services and fitted as a continuous variable to provide an index of season. Temperature values from weather stations at Mata Mata, Twee Rivieren and Nossob camps were averaged. Values are the same for all blocks for each point in time and thus only represent temporal variations. Using temperature in this way with a cool dry season and a warm wet season provides a seasonal indicator of how wildebeest numbers fluctuate within the riverbeds in the KTP.

Predator density

Predator density and distribution may play an important role in directly shaping which areas wildebeest use. Monthly counts of lion, cheetah, leopard and spotted hyena from the SANParks census data were summed to create a predator density variable to predict wildebeest presence. I do this because individual monthly counts of each species were very low.

3.2.3 Analyses

Spatially explicit conditional autoregressive models were fitted to identify the environmental drivers of wildebeest landscape use within the riverbeds of the KTP. Wildebeest landscape use was modelled using a binomial distribution, with wildebeest presence or absence in a block scored based on whether two or more wildebeest were recorded in that block. A threshold of two individuals for scoring ‘presence’ was used to reduce the influence of sedentary lone bulls on the analyses. These territorial bulls show high fidelity to a particular region despite variation in environmental conditions (Von Richter 1972, Knight 1991). NDVI, temperature, water status, tree density, riverbed width and predator density were fitted as independent variables to predict wildebeest distribution using integrated nested Laplace

approximation (INLA: Rue *et al*. 2009). The random effects structure used in the models accounted for spatial autocorrelation among neighbouring blocks within months and for the influence of repeated measures on the same blocks across months. Model comparisons were based on the Watanabe-Akaike Information Criterion (WAIC), with models with WAIC values that differed by two or more considered significantly different. All R^2 values for correlations between predictor variables were less than 0.1 (Supplementary Table S3.1). All analyses were conducted using the software program R v. 3.3.1 (R Core Team 2016).

The analysis was started by first fitting the full set of models comprising all additive permutations of NDVI, temperature, water status, tree density and riverbed width (i.e. from single to five variable models). The best model was selected based on WAIC, and then used as a basis to test for an interactive effect between water status and NDVI, temperature and tree density respectively. Fitting these interactions provides a test of whether the water status of a block modifies the more general effect of forage, season or shade on the wildebeest presence. Finally, predator density was fitted in the best additive model to assess the evidence for a direct effect of predators on wildebeest landscape use.

3.3 Results

3.3.1 Model selection

Five of the additive models were found to have equivalent support based on Watanabe-Akaike Information Criterion (WAIC) values (Table 3.1). Tree density, NDVI, water status, temperature and river width each featured in at least three of these statistically equivalent models, with only NDVI featuring in all five models. This suggests that each of the five predictor variables has an important influence on wildebeest landscape use patterns, but that only small improvements in overall model fit are obtained once more than three predictor variables are included in a model. In addition to the statistical support for each predictor, there is also a case for preferring the full model from an ecological perspective, because the inclusion of each predictor was based on a reasonable expectation that it would have an influence on wildebeest landscape use patterns, and parameter estimates are consistent with these expectations. Therefore, the additive model including all five predictor variables was selected as the 'best model' for use in subsequent analyses, and is described in full below.

Table 3.1. *Model comparisons among the full set of additive models for the five environmental predictors of landscape use by wildebeest, based on the Watanabe-Akaike Information Criterion (WAIC). The difference between the WAIC for a model and that of the model with the lowest WAIC value is shown in the in Δ WAIC column.*

Model	WAIC	Δ WAIC
Trees + NDVI + Water + Temperature + River width	2315.17	0
NDVI + Water + River width	2315.51	0.34
Trees + NDVI + Water + Temperature	2315.98	0.81
Trees + NDVI + Temperature + River width	2316.74	1.57
NDVI + Temperature + River width	2316.97	1.80
Trees + Water + Temperature + River width	2335.69	20.52
Trees + Water + Temperature	2334.99	19.82
Water + Temperature + River width	2336.27	21.10
NDVI + Water + Temperature	2337.1	21.93
NDVI + Temperature	2337.67	22.50
Trees + NDVI + Temperature	2336.95	21.78
Temperature + River width	2339.92	24.75
Trees + Temperature + River width	2340.26	25.09
Trees + Temperature	2351.87	36.70
Water + Temperature	2351.99	36.82
Temperature	2352.56	37.39
NDVI + Water + River width	2356.56	41.39
Trees + NDVI + Water + River width	2356.22	41.05
Trees + NDVI + Water	2356.53	41.36
Trees + NDVI + River width	2357.8	42.63
NDVI + River width	2358.06	42.89

Trees + Water + River width	2372.7	57.53
Water + River width	2372.98	57.81
Trees + River width	2374.67	59.50
Trees + Water	2373.46	58.29
River width	2374.78	59.61
NDVI + Water	2379.5	64.33
Trees + NDVI	2379.32	64.15
NDVI	2380.06	64.89
Trees	2319.69	76.52
Water	2319.83	76.66

3.3.2 Drivers of wildebeest distribution patterns in the Auob and Nossob rivers

Wildebeest occurrence in the dry riverbeds of the KTP is determined by shade, forage, water, temperature and river width (Table 3.2). Wildebeest occurred more frequently in areas with higher tree densities where shade availability is thus likely to be higher (Fig. 3.1A). Increasing tree density from 25% to 75 % of the observed range of values (i.e. from 17 to 36 trees/km^2) while keeping all other continuous variables at their mean value resulted in an 11 % increase (i.e. from 0.40 to 0.51) in the probability of observing wildebeest in a block with fresh water. Similarly, NDVI was positively associated with wildebeest occurrence (Fig. 3.1B), with the likelihood of wildebeest presence increasing by 6 % (0.42 to 0.48) over the interquartile range of observed NDVI values (i.e. NDVI: 0.168 to 0.221).

Temperature was negatively associated with wildebeest presence (Fig. 3.1C). Over the interquartile range of temperature wildebeest occurrence decreased by 10%, demonstrating that there is some level of movement out of the riverbeds during the hot, wet season months. This effect is evident in the raw census data (Fig. 3.2) that show lower wildebeest numbers in the KTP when wet season temperatures peak between November and February. Riverbed width also plays an important role in wildebeest habitat preference, with support for a marked decrease in animal density in narrow areas of the riverbed (Fig. 3.1D). Increasing riverbed

width over the interquartile range (i.e. 165 metres to 377 metres) resulted in a 23% (0.35 to 0.58) increase in wildebeest occurrence. Finally, wildebeest showed a clear preference for areas with fresh water (median = 50.2%) compared to areas with salty (34.8%) or no water (29.8%; Fig. 3.1E).

***Table 3.2**. Median and 95% confidence intervals of parameter estimates for the environmental variables as predictors of wildebeest distribution patterns in the Kalahari Transfrontier Park. Tree density (trees/km^2), NDVI, water status (none, salty or fresh), temperature (°C) and river width (m) were used to model the presence/absence of wildebeest using a binomial distribution. Conditional autoregressive models were fitted in INLA and account for spatial autocorrelation and repeated measures within a Bayesian framework. Statistical support for a model term is obtained where the credible interval (0.025 to 0.975 quantile range) for the parameter estimate does not overlap zero.*

Environmental variable	Model term	0.025 quantile	0.5 quantile	0.975 quantile
	Intercept	-1.0040	-0.8568	-0.7152
Shade availability	Tree density	0.3031	0.3027	0.4333
Forage availability	NDVI	0.1097	0.2094	0.3093
Water status	None	0	0	0
	Salty	0.2293	0.4345	0.6408
	Fresh	0.2124	0.7040	1.2005
Seasonal migration	Temperature	-0.4108	-0.3124	-0.2153
Predator visibility	River width	0.3670	0.5657	0.7608

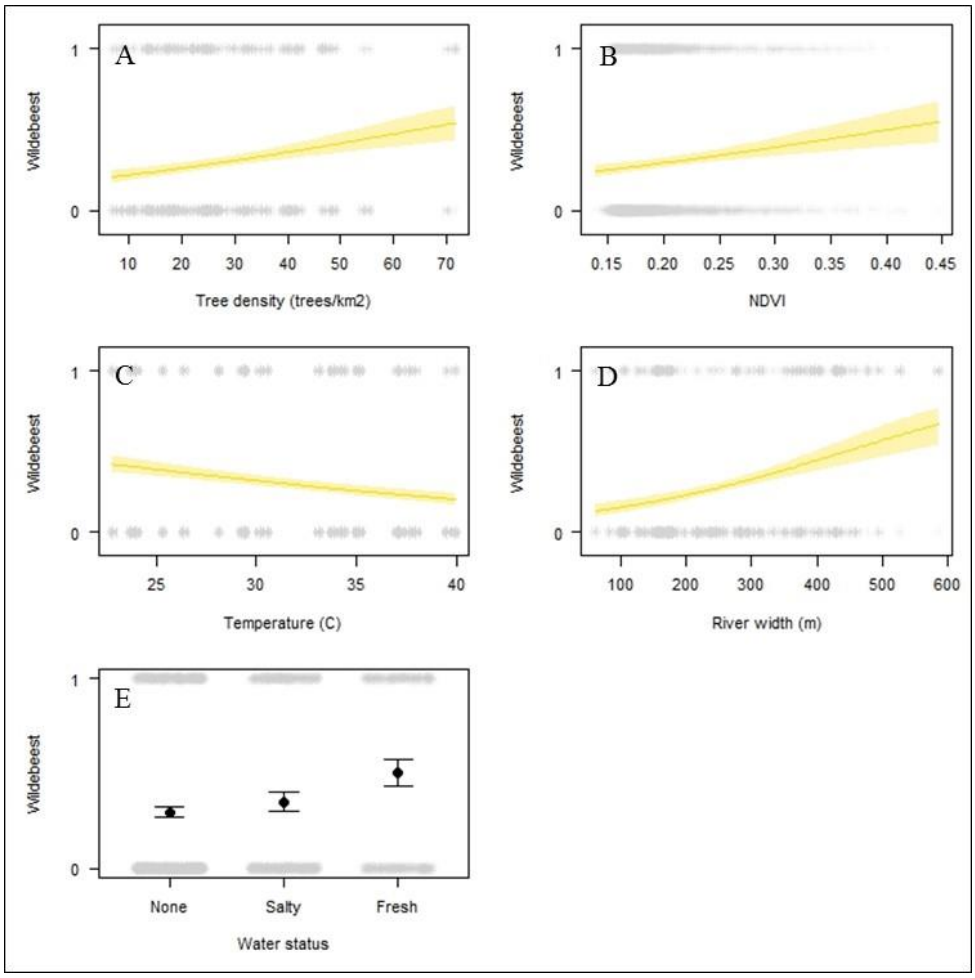

Fig. 3.1. *Probability of wildebeest presence (y-axis) in relation to environmental variables as estimated by the best additive model: A) shade cover as estimated by tree density, B) forage availability as estimated by NDVI, C) temperature (°C), which serves as a proxy for cool winter dry seasons to hot summer wet season conditions, D) predator visibility as approximated by river width (m), and E) water status in a study block (none: no water, salty: water with > 3% salinity, fresh: water with < 3% salinity). Grey points represent the raw data, with median model predictions and the associated 95% credible interval estimate range shown by the solid yellow line and shaded region, respectively.*

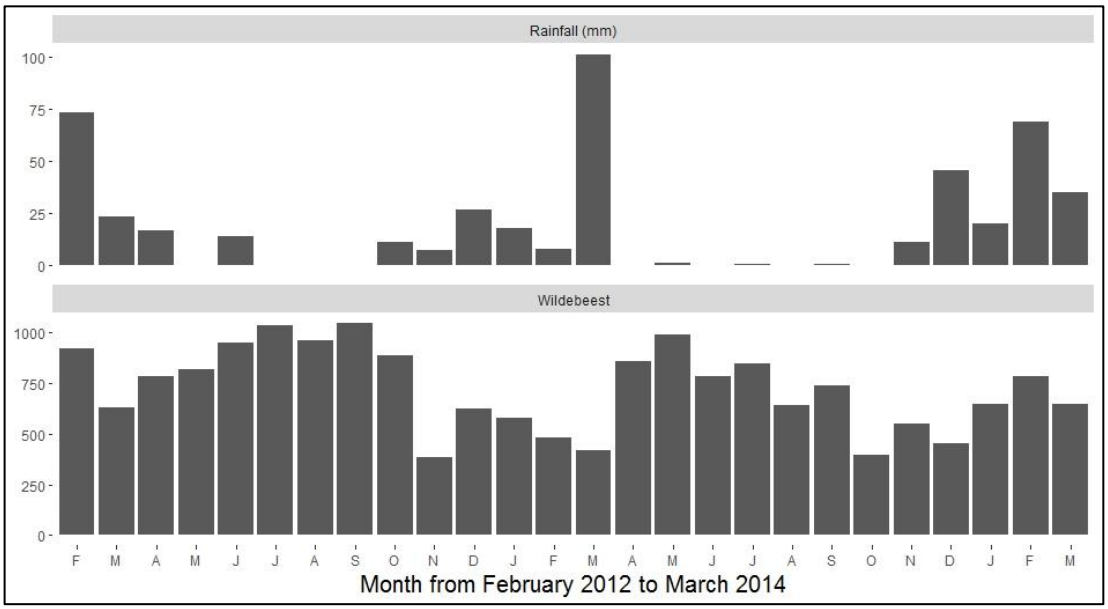

Fig. 3.2. *Total number of wildebeest recorded for each month relative to monthly rainfall averages for the 26 month study period. Wildebeest numbers were obtained from census data and reflect animal numbers in the riverbeds of the Auob and Nossob rivers. Rainfall averages were calculated from weather stations at Mata Mata, Twee Rivieren and Nossob (SAWS).*

3.3.3 Interaction with water status

There was support for an interactive effect between water status and NDVI, and water status and temperature (Table 3.3). However, there was no support for an interaction between water status and tree density. The interactive effect between water status and NDVI shows that the higher use of areas with fresh water is largely independent of foraging conditions (Fig. 3.3A). By contrast, areas with salty or no water are little used when NDVI values are low, but become more likely to be used by wildebeest as NDVI increases. Overall, wildebeest are more likely to be observed in the riverbed when temperatures are cooler during the dry season, regardless of the water status of the area (Fig. 3.3B). The interaction between temperature and water demonstrates a relatively greater difference in the seasonal use of areas with fresh water compared to areas with salty or no water (i.e. a steeper negative slope in Fig. 3.3B), with all areas showing similarly low use when temperatures are higher during

the wet season. It is also interesting to note that in both the NDVI and temperature interaction plots, wildebeest usage of areas with salty water is more similar to areas with no water than they are to areas with fresh water.

Table 3.3. *Model comparisons between the full additive model (i.e. Trees + NDVI + Water + Temperature + River width) of landscape use by wildebeest and those including the interaction of water status with tree density, NDVI and temperature respectively. Comparisons are based on the Watanabe-Akaike Information Criterion (WAIC), and the difference between the model WAIC and the WAIC for the full additive model (2315.17) is shown in the Δ WAIC column.*

Model	**WAIC**	**Δ WAIC**
Full model + Water:NDVI	2310.87	-4.30
Full model + Water:Temperature	2311.92	-3.88
Full model + Water:Tree density	2315.20	0.03

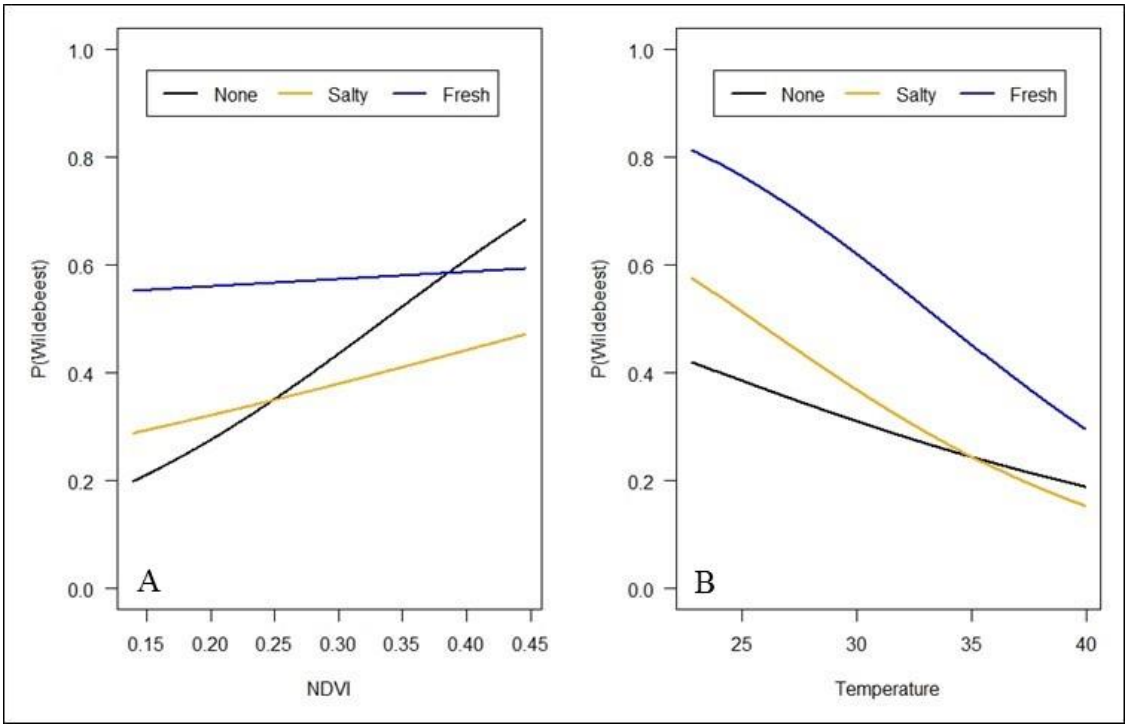

Fig. 3.3. *Exploring the interactive effects between water and NDVI (A), and water and temperature (B) on wildebeest presence when all other environmental variables are equal to zero. Black lines represent areas with no water, blue lines represent areas with fresh water and areas with saline water are represented by yellow lines. Y-axis values are the probability of wildebeest presence.*

3.3.4 Predator density

There was no support for including predator density as an additional predictor in the full model (WAIC = 247.03; ΔWAIC = 163.86 vs. full model), with the parameter estimate for the effect of predator density not being distinguishable from zero (credible interval: -0.078 to 0.121) (Supplementary Table S3.1).

3.4 Discussion

My results show that the distribution of wildebeest in the Auob and Nossob riverbeds is shaped by a range of environmental variables, including water availability and quality, forage availability, shade and river width. My results also show that there is a seasonal dispersal of wildebeest out of the riverbeds and into the surrounding regions during the hotter, wetter months. While regularly spaced waterholes are the key management intervention allowing for the establishment of a sedentary wildebeest population in the KTP (Eloff 1966; Bothma, 1972; Mills & Retief 1984; Mills & Retief 1984b; Knight 1991), there is considerable variation in wildebeest distribution in the riverbeds through the seasonal cycle.

It is not only the availability of water but the quality of water that is a driver for wildebeest distribution in this system. Wildebeest are a water dependant species that remain less than 5 km from water whenever possible, particularly in the dry season (Western 1975; Knight 1991; Smit *et al*. 2007). The regular spacing of waterholes along the Auob and Nossob riverbeds (average of one waterhole every 10.5 km) shows that water is accessible to wildebeest in almost all sections of the riverbed. Despite this, the resident population of wildebeest do not occur evenly across the riverbeds and their distribution within this habitat is also driven in part by water quality. While access to surface water has made it possible for wildebeest to remain in the area throughout the year, other environmental factors appear to be very important for driving wildebeest habitat preference within the riverbeds.

Forage availability also determines wildebeest distribution within the riverbeds of the KTP, with animals making greater use of areas with higher NDVI. In an arid savannah region like the KTP, where rainfall is distinctly seasonal, the moisture content of plants is much higher during the wet season (i.e. when NDVI is high), which reduces an animal's reliance on drinking water (Williamson *et al*. 1988; Hendricks *et al*. 2005). This explains both the

greater use of areas with salty or no water when NDVI is high, and also the seasonal dispersal of wildebeest out of the riverbeds during the growing season. Wildebeest are thus responsive to variation in foraging conditions, with animals showing a tendency to seek out areas where they can better meet their nutritional requirements.

Shade cover has a clear positive effect on wildebeest presence. My results show that wildebeest are more likely to use sections of the riverbed that have a high density of trees relative to sections in which tree cover is sparse. In this context, using tree density as an indication of shade is reasonable as wildebeest are unlikely to browse on large trees. These animals are also known to make use of shade to escape the intense midday heat (Knight 1991; Ben-Shahar & Fairral 1987), particularly given that they spend long parts of the day ruminating and largely inactive (Ben-Shahar & Fairall 1987). This suggests that wildebeest preference for areas with more shade in the KTP is driven by thermoregulation. My results also show no interactive effect between water availability and shade, demonstrating that wildebeests are preferentially seeking areas with more shade regardless of available water (Sunday *et al.* 2012).

This analysis shows that part of the wildebeest population is moving out of the riverbeds during the growing season. While some animals are likely to move into the dunes, I expect most to move eastwards across the KTP border as suggested by early observations of wildebeest movement in the region (Eloff 1961; Bothma 1972; Williamson *et al.* 1988). Unfortunately the SANParks census data counts were only made in the riverbed and as such, the location of these animals once they have left the riverbed did not form part of this study. It is however possible that those animals leaving the riverbed do so in search of better quality and/or more abundant forage, with the constraint of retaining access to drinking water partially relieved by higher forage moisture content (Williamson *et al.* 1988). Ephemeral surface water present during the summer rainy season may also be important in facilitating these seasonal movements (Williamson *et al.* 1988; Knight 1991).

My results also show that sections of the riverbed that are wide and open are more likely to be used by wildebeest. My model results do not demonstrate that this is due to the lack of cover in these areas, leading to higher predator visibility and thus reduced predation risk (Valeix *et al*. 2009; Riginos 2015). Associated with changes in river width are shifts in the density of shrub cover, with the narrower southern Nossob and Auob regions tending to have

a relatively high density of large *Galenia africana* (van Rooyen *et al.* 2008; Chapter 2). The combination of decreased river width and high shrub cover mean that these areas offer more cover for predators (Thaker *et al.* 2011). However, differences in shrub cover are not the only vegetation change associated with riverbed width. Wider sections of the riverbed also have a larger area of short grass communities (van Rooyen *et al.* 2008), a preferred habitat for wildebeest in the region (Knight 1995; van Rooyen *et al.* 2008).Rather than minimising predation risk in a landscape of multiple predators, shifts in grass community composition may explain wildebeest preference for wider sections of the river (Thaker *et al.* 2011). The lack of support for a predator term in my model does not necessarily imply that predators have no influence on wildebeest distributions in the KTP, and the importance of predation in structuring herbivore communities in other regions (e.g. Sinclair 1985) is clear. Analysing predator effects using a smaller spatial grain may shed more light on the role of predators in this particular system.

In conclusion, the results of this chapter show that it is not only available water that determines wildebeest density but rather a combination of availability and quality of water along with forage conditions, the amount of shade and possibly vegetation structure that influences predator detectability. However, my model results do not identify any direct association between predator abundance and wildebeest presence.

CHAPTER 4

Wildebeest feeding ecology

4.1 Introduction

In arid savannah systems such as the KTP, highly seasonal and spatially sporadic rainfall patterns lead to temporal and spatial fluctuations in forage quality and quantity (Werger & Leistner 1975; van Rooyen & van Rooyen 1998). These changes in available forage have a direct effect on the movement of grazing ungulates in the region, particularly those whose movements are restricted by access to permanent surface water (Knight 1991). The sedentary behaviour of blue wildebeest in the KTP and their dependence on surface water may therefore lead to changes in the diet and subsequent health of these grazing ungulates (Mills & Retief 1984; Mills & Retief 1984b). As the feeding habits of grazers can reflect resource availability and preference, a dietary determination can provide an understanding of habitat condition and how a sedentary population of these animals may affect vegetation structure (Grant *et al*. 2000).

The semi-arid KTP is at the southern edge of the blue wildebeest current distribution range, and is also one of the driest environments in which these large grazers occur. The establishment of a largely sedentary population of wildebeest in this environment has also been directly facilitated by the artificial provision of drinking water (Mills & Retie 1984; Mills & Retief 1984b). As a result, it is possible that the feeding ecology of the KTP wildebeest population may differ from populations that still follow historical migration patterns, or where the species occurs in more mesic environments. Wildebeest are predominantly grazers, with grass constituting about 95% of their diet in areas like the Kruger National Park (Codron et al. 2005), Serengeti (Gwynne & Bell 1968) and southern Kenya (Ego et al. 2003, Owaga 1975). Despite this, wildebeest are known to incorporate some C_3 vegetation into their diet. In the Hluhluwe-iMfolozi Park, for example, wildebeest have been recorded consuming as much as 20% C_3 vegetation during the dry season (Botha & Stock 2005). In the KTP, the distribution of wildebeest is restricted by access to fresh drinking water, particularly during the dry season (Chapter 3). It is therefore possible that wildebeest in this system may be forced to change their predominantly grass-dominated diets based on the characteristics of the vegetation within daily foraging range from these waterholes.

Stable isotope analysis of the dung of savannah herbivores is a useful tool for providing accurate information about the relative proportion of grass (C_4 photosynthesis) to browse (forbs, trees and shrubs that use C_3 photosynthesis) as well as the nutritional status of an animal's diet (Vogel 1978; Lee-Thorp & van der Merwe 1987; Sponheimer *et al*. 2003; Codron *et al*. 2005). The C_3 and C_4 photosynthetic pathways differ in ability to assimilate CO_2 from the atmosphere, with the C_4 photosynthetic pathway being more efficient (Lee-Thorp 2008; Sealy 2001). Plants using the C_3 photosynthetic pathway discriminate strongly against the heavier ^{13}C isotope during CO_2 fixation, with the consequence that plants using the C_4 photosynthetic pathway assimilate a relatively higher proportion of the heavier ^{13}C isotope. Ratios of ^{13}C:^{12}C in plant material are determined using an isotope ratio mass spectrometer with results relative to a carbonate standard expressed with a δ notation in parts per mil (ppm or ‰). Plants using the C_3 photosynthetic pathway have $\delta^{13}C$ values averaging around -26.5‰ while plants using the C_4 pathway have $\delta^{13}C$ values around -12.5‰ (Vogel 1978; Cerling *et al*. 1997). These differences in carbon isotope ratios between C_3 and C_4 photosynthesis are laid down in the tissues and dung of animals, making it possible to determine the proportion of C_4 (grass) and C_3 (shrub/tree) vegetation in their diet using relatively simple mixing models (Vogel 1978; Cerling & Harris 1999; Codron *et al*. 2005; February *et al.* 2017).

Failure to meet nutritional requirements with available forage can result in the deteriorating body condition of an animal with potentially negative impacts on reproductive success and survival (Hempson *et al*. 2015). A determination of the crude protein content of an animal's diet is an important measure of forage quality, with a threshold level of 7-8 % crude protein generally considered necessary to meet the maintenance requirements of large-bodied ruminants (e.g. Beekman & Prince 1989; Cooper *et al.* 1988). Determining the crude protein content of different grass species and exploring the seasonal and regional variation in forage quality in the KTP provides important information on the forage conditions available to grazers in this semi-arid environment. This, in conjunction with the information on diet from stable isotope analysis of wildebeest dung, can provide insights into how wildebeest shift their diet to best meet nutritional requirements through the seasonal cycle (Codron *et al*. 2007).

In this chapter I use stable carbon isotope ratios and percent nitrogen content of grass leaf material to explore seasonal variations in forage quality in the KTP, and how this may differ between areas with high and low use by wildebeest. I use a similar analysis on wildebeest dung to determine the amount of browse (C_3) and graze (C_4) in the diet and how this changes both spatially and temporally. Using the percentages of nitrogen in plant material I make a determination of the crude protein content to evaluate change in nutritional status (Cooper *et al.* 1988). Finally I assess whether the amount of grazing on different grass species reflects their abundance, and whether these preferences are related to my estimates of forage quality for different grass species. Note that these final analyses are not specific to wildebeest, and instead provide a description of the forage selection patterns of the wider grazer community.

4.2 Methods

4.2.1 Identifying high and low use areas

I used the monthly SANParks game surveys conducted between February 2012 and March 2014 (see Chapter 2) to identify areas with high and low use by wildebeest in the Auob and Nossob riverbeds. I do this by calculating the average number of wildebeest in each of the 85 contiguous 5 X 0.9 km blocks that I had divided the full length of the Auob and Nossob riverbeds into (as described in Chapter 3). The five blocks with the highest and lowest average wildebeest count were defined as the high and low use regions respectively. These 10 blocks were all located in the Nossob riverbed, with high use areas averaging > 15 wildebeest each month, and low use areas averaging < 5 wildebeest. Red hartebeest and springbuck showed similar high and low use patterns, but not gemsbok (Fig. 4.1).

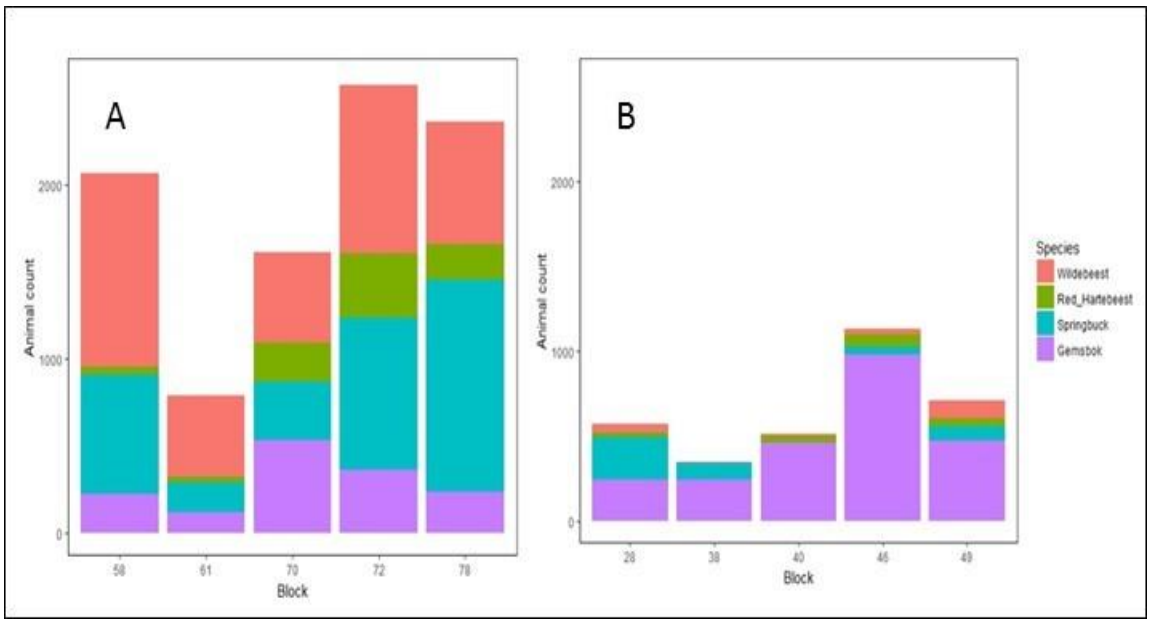

Fig. 4.1. *Total sum of animal counts for each study block over the 26 month census period. Low use blocks (A) were defined as having a monthly average of <5 wildebeest over the census period, and high use blocks (B) as having >15 wildebeest recorded each month.*

4.2.2. Dung and grass sampling

Data were collected during two fieldtrips from January 18th to February 5th 2015 (wet season) and October 18th to November 5th 2015 (dry season). For both seasons eight transects spaced 500 m apart were walked in each of the ten study blocks, stretching across the river from the mid slope of one bank to the mid slope of the opposite bank. Due to the nature of the river these transects varied considerably in length. Counts of all grass species within one metre of each sampling point and any evidence of grazing were recorded at 5 m intervals along the entire length of each transect. A simple grazing classification of grazed/ungrazed was used to assess the grazing evidence on each grass tuft. While these results cannot specifically be attribute to wildebeest it does give an indication of grass community composition and how heavily grazed specific species were in each study block. Two samples (clipped at 1 cm above ground) of each of the three most common grass species were obtained from each of the ten blocks for both seasons with green specimens sampled whenever possible (60 grass samples). One sample of the shrubs *Monechma incanum* and/or *Monechma genistifolium* subs. *austral* were also collected from each block to obtain a regionally specific C_3 end point (ten shrub samples). These two species were sampled because they showed the most utilization by herbivores, and are known to be browsed by wildebeest in this region (*personal*

observation). Three independent fresh dung samples were also collected from each block with the first fresh dung sample encountered on each transect collected, providing three independent dung samples from each block.

4.2.3. Lab analyses

All leaf and dung samples were dried to a constant weight at 70°C before grinding to a fine powder using a Retsch MM 200 ball mill (Retsch, Haan, Germany) for leaves and a Wiley Mill (Thomas Scientific Swedesboro, New Jersey, U.S.A.) for dung samples. A 2-3 mg subsample (Grass: n=120; Shrub: n=10; Dung: n=60) was then combusted in a Flash 2000 organic elemental analyser and the gases passed to a Delta V Plus isotope ratio mass spectrometer (IRMS) via a Conflo IV gas control unit (Thermo Scientific, Bremen, Germany). The results were calibrated relative to atmospheric N_2 for nitrogen and Pee-Dee Belemnite for carbon as which also corrects for drift in our in house reference gas. Deviation from the standard is denoted by the term δ and the results expressed as parts per thousand (‰). Precision of duplicate analysis is 0.1 ‰ for carbon and 0.2 ‰ for nitrogen (February *et al.* 2011).

4.2.4 Analyses

A dual-endpoint mixing model was used to convert faecal $\delta^{13}C$ values to estimates of percent C_4 grass intake of wildebeest (e.g. Sponheimer *et al.*, 2003; Codron *et al.*, 2007):

$$\frac{\left(\delta^{13}C_{C3plant} + \Delta^{13}C - \delta^{13}C_{animal}\right)}{\left(\delta^{13}C_{C3plants} - \delta^{13}C_{C4plants}\right)}$$

Where $\Delta^{13}C$ is the isotopic discrimination between diet and faeces, here taken to be – 0.9‰ (Sponheimer *et al.* 2003). While many studies use the global averages for $\delta^{13}C$ values of C_3 and C_4 plants (-27.0 and -12.5‰; Cerling *et al*. 1997), I use endpoint values that are seasonally and regionally specific to the species in my study area. This is because stable isotope ratios of plants show considerable geographic variation and local endpoint values ensure accurate estimates of percent C_4 grass intake. Wet and dry season $\delta^{13}C$ values for grasses were used while shrub endpoint values were calculated from 10 dry season samples only primarily because I did not expect any seasonal changes in non-deciduous shrub $\delta^{13}C$ values.

Forage and diet quality were quantified using C:N ratios and estimates of crude protein levels. C:N ratios were calculated by dividing the carbon content of each sample by the nitrogen content. I use percent nitrogen content of leaves and dung multiplied by 6.25 to obtain a value for crude protein content of the leaves (Cooper *et al*. 1988). Differences in forage quality (leaf C:N and crude protein), the amount of C_4 grass in wildebeest diets, and wildebeest diet quality (dung crude protein) were compared among season (dry and wet) x wildebeest use (high and low) categories using ANOVA statistical tests. Pairwise comparisons among categories were made using Tukey HSD tests where statistical differences were detected.

I quantified the grass species preference of all large herbivores using grass species counts (availability) and grazing evidence (use) for each season. Pearson's chi-squared tests were used to test whether observed grass usage was consistent with a null hypothesis that expected use would be directly proportional to availability. Dry and wet season data were analysed separately, with data from high and low use blocks being combined for each season. Grass species that made up less than 1% of the total sample were excluded. This was done to reduce the loss of statistical power caused by unbalanced marginal totals with some categories only having very few observations. Chi-square post hoc tests (with false discovery rate correction, to account for type I errors arising from multiple comparisons; chisq.post.hoc function in fifer package in R; Fife 2017) were used to investigate pairwise differences among species. A preference index was then assigned to each species by dividing the observed use by the expected use, centering this ratio on zero (i.e. by subtracting 1), and multiplying by 100 to give a percentage. This index accounts for differences in abundance of grass species. Similar indices have been used when measuring diet selection among terrestrial herbivores (Norbury & Sanson 1992). This preference index was then used to test the relationship between grass species preference and quality (i.e. C:N and crude protein) using a Spearman rank correlation test. All statistical analyses were conducted in R (R v. 3.3.1 (R Development Core Team 2016).

4.3 Results

***Table 4.1**. Wet season average δ^{13} C, δ^{15} N, %C and %N of the dominant grass species from the study site, with standard deviation in brackets.*

Species	δ^{13}C	δ^{15}N	%C	%N	No. of samples
Chloris virgata	-14.6	6.4	39.6	1.8	2*
Enneapogon desvauxii	-14.9 (± 0.5)	5.2 (± 1.3)	39.2 (± 3.0)	2.0 (± 0.4)	14
Eragrostis porosa	-14.7	4.6	41.0	2.0	2*
Panicum coloratum	-13.7 (± 0.5)	6.2 (± 0.4)	39.4 (± 2.1)	1.9 (± 0.6)	6
Schmidtia kalahariensis	-14.4 (± 0.5)	4.4 (± 2.3)	39.0 (± 3.7)	1.8 (± 0.9)	18
Stipagrostis ciliata	-14.6 (± 0.1)	5.8 (± 1.5)	42.5 (± 0.7)	1.5 (± 0.2)	4
Stipagrostis obtusa	-14.5 (± 0.4)	2.1 (± 0.8)	38.4 (± 6.1)	1.3 (± 0.3)	8
Tragus racemosa	-14.6 (± 0.4)	4.7 (± 0.7)	37.8 (± 1.9)	2.7 (± 0.4)	6

* sample size too small to calculate standard deviation.

***Table 4.2**. Dry season average δ^{13} C, δ^{15} N, %C and %N of the dominant grass and shrub species from the study site with standard deviation in brackets.*

Species	δ^{13}C	δ^{15}N	%C	%N	No. of samples
Aristida congesta	-14.1	4.5	42.1	0.6	2*
Chloris virgata	-14.4 (± 0.3)	5.8 (± 0.8)	39.4 (± 0.7)	0.9 (± 0.3)	8
Enneapogon desvauxii	-14.4 (± 0.3)	4.0 (± 1.3)	39.0 (± 3.3)	0.9 (± 0.2)	16
Eragrostis annulata	-14.6 (± 0.2)	4.4 (± 0.9)	41.8 (± 0.3)	0.7 (± 0.1)	4
Eragrostis porosa	-14.7	3.2	42.0	0.6	2*
Schmidtia kalahariensis	-13.9 (± 0.3)	2.0 (± 2.1)	40.8 (± 1.0)	0.5 (± 0.2)	12
Stipagrostis ciliata	-14.7 (± 0.4)	2.0 (± 1.4)	43.2 (± 0.0)	0.5 (± 0.1)	4
Stipagrostis obtusa	-14.0 (± 0.3)	1.8 (± 1.5)	38.7 (± 2.2)	0.7 (± 0.1)	12
Monechma genistifolium	-24.7 (± 0.4)	7.2 (± 0.5)	37.3 (± 1.1)	1.9 (± 0.3)	8
Monechma incanum	-25.2	9.8	41.5	2.1	2*

* sample size too small to calculate standard deviation.

4.3.1 Stable isotope ratios

Stable isotope ratios of the dominant grass species in the study blocks show little seasonal variation in δ^{13} values. However, there is a noticeable increase in %N during the wet season for all sampled species and a corresponding decrease in C:N ratios. *Eragrostis porosa* and *Enneapogon desvauxii* have the highest wet season %N content while dry season %N is lowest in *Schimdtia kalahariensis* and S*tipograstis ciliate* respectively (Tables 4.1 and 4.2).

4.3.2 Variations in seasonal and regional grass quality.

Forage quality differed among season by use categories both when quantified as crude protein ($F_{3, 116} = 51.65$, $P < 0.001$) and as C:N ($F_{3, 116} = 24.61$, $p < 0.001$). A post hoc Tukey test shows that crude protein levels were higher in the wet season than in the dry season (overall means: wet = 11.7% vs. dry = 4.5%; $P < 0.05$), and that during the wet season, crude protein was higher in high use areas that in low use areas (wet-high: 12.9% vs. wet-low: 10.5%; Fig. 4.2; $P < 0.05$). There was no difference in crude protein levels between high and low use areas during the dry season. Similarly, C:N was higher during the dry season than in the wet season (i.e. lower forage quality; overall means: wet = 27.4 vs dry = 65.1; $P < 0.05$), but there was no difference between high and low use areas in either the wet or dry season (Fig. 4.3).

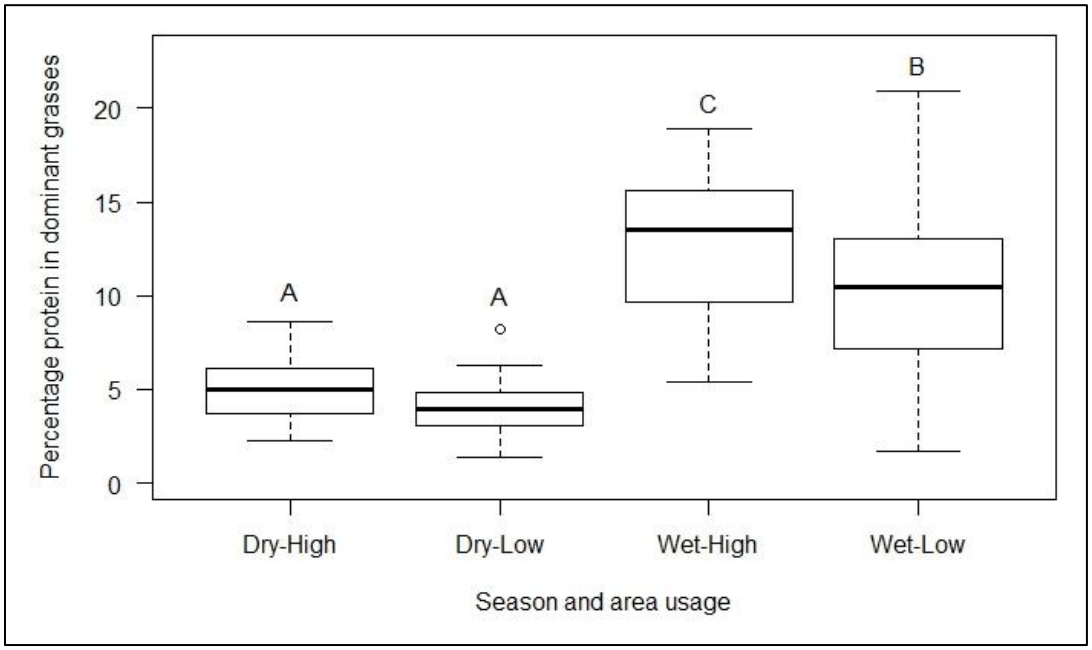

Fig. 4.2. *Seasonal changes in crude protein (%) of the three most abundant grass species in each block showing the decrease in grass nutrition in the dry season. Analyses were performed*

on log transformed data to meet the assumptions of an ANOVA. Boxes sharing letters do not differ at the 95% confidence level.

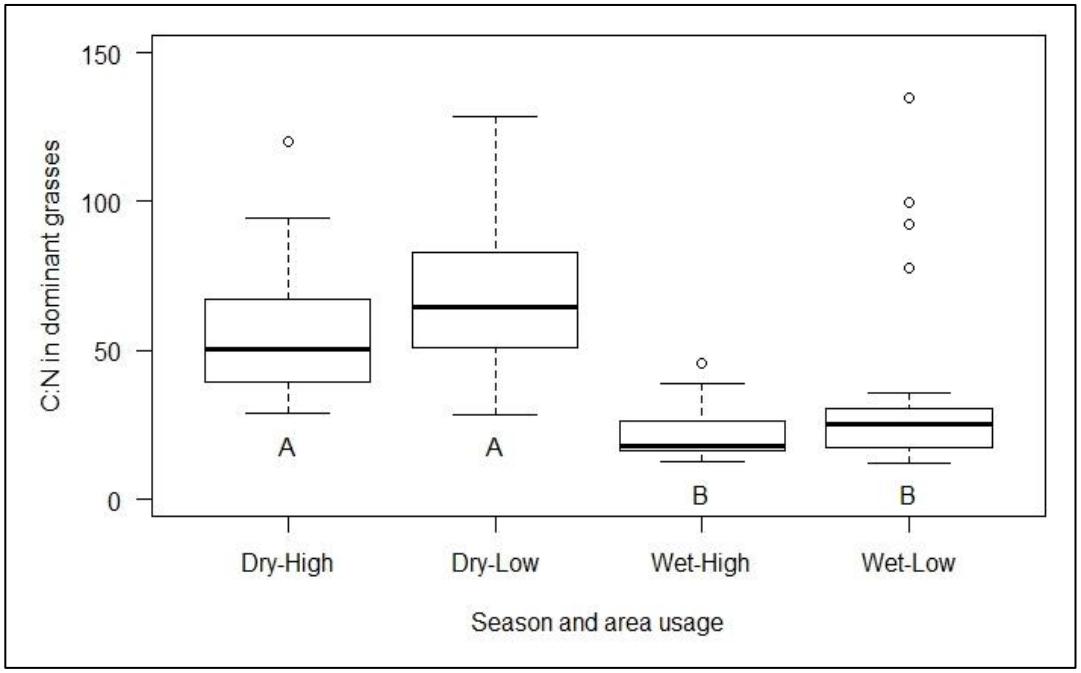

Fig. 4.3. *Seasonal changes in C:N ratio of the three most abundant grass species within each block in both the wet and dry season. Analyses were performed on log transformed data to meet the assumptions of an ANOVA. Boxes sharing letters do not differ at the 95% confidence level.*

4.3.3 Proportion of C_3/C_4 in wildebeest diet

The localized end member $\delta^{13}C$ values used for the dual end point mixing models were:

Wet season:

$\delta^{13}C_{shrub}$ = -24.8‰ (note that shrub samples were only collected in dry season)

$\delta^{13}C_{grass}$ = -14.5‰ (N = 60)

Dry season:

$\delta^{13}C_{shrub}$ = -24.8‰ (N = 10)

$\delta^{13}C_{grass}$ = -14.3‰ (N = 60)

Overall, my results show that grass constituted 74.0 ± 9.5 % (mean ± standard deviation) of the diet of wildebeest, but that there were differences among season x use categories ($F_{3, 55}$ = 8.045, P<0.001) A posthoc Tukey test reveals that these differences are due to the particularly low grass intake during the dry season in the low use areas (65.8 %; $p < 0.05$, Fig. 4.4) compared to the other season x use categories (dry-high = 76.4%, wet-low = 74.1% and wet-high = 79.7%).

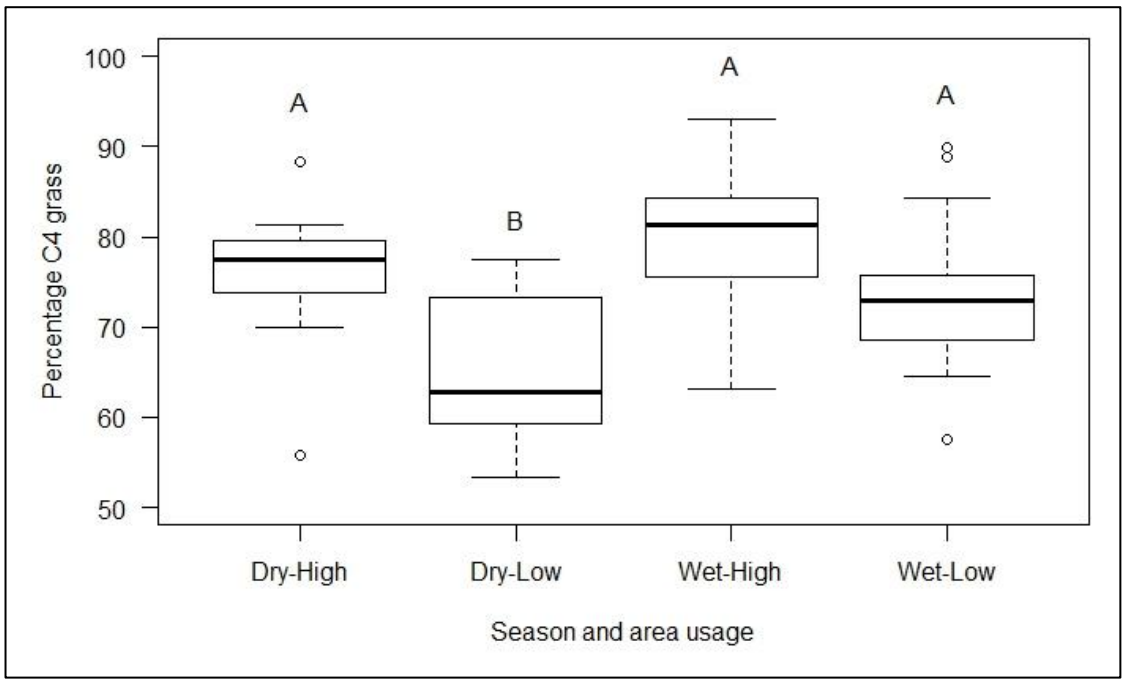

Fig. 4.4. *The seasonal consumption of grass by wildebeest in the KTP showing the increase of browse (C_3) in the diet at the end of the dry season in the low use area. The line within the boxes represents the median while the lower and upper limits are the 75th and 25th percentiles. The lines extending from each end of the boxes show the non-outlier range. Boxes sharing letters do not differ at the 95% confidence level.*

4.3.4 Seasonal and regional variations in the quality of wildebeest diet.

There was no evidence for any differences in the percentage crude protein in wildebeest dung among season x use categories ($F_{3, 55}$ = 1.083; P = 0.16). Wildebeest dung crude protein levels were therefore maintained within a narrow range (i.e. between 8-10 %) throughout the year and across regions (dry-low = 8.3%, dry-high = 8.9%, wet-low = 9.7%, wet=high = 9.7%; Fig. 4.5).

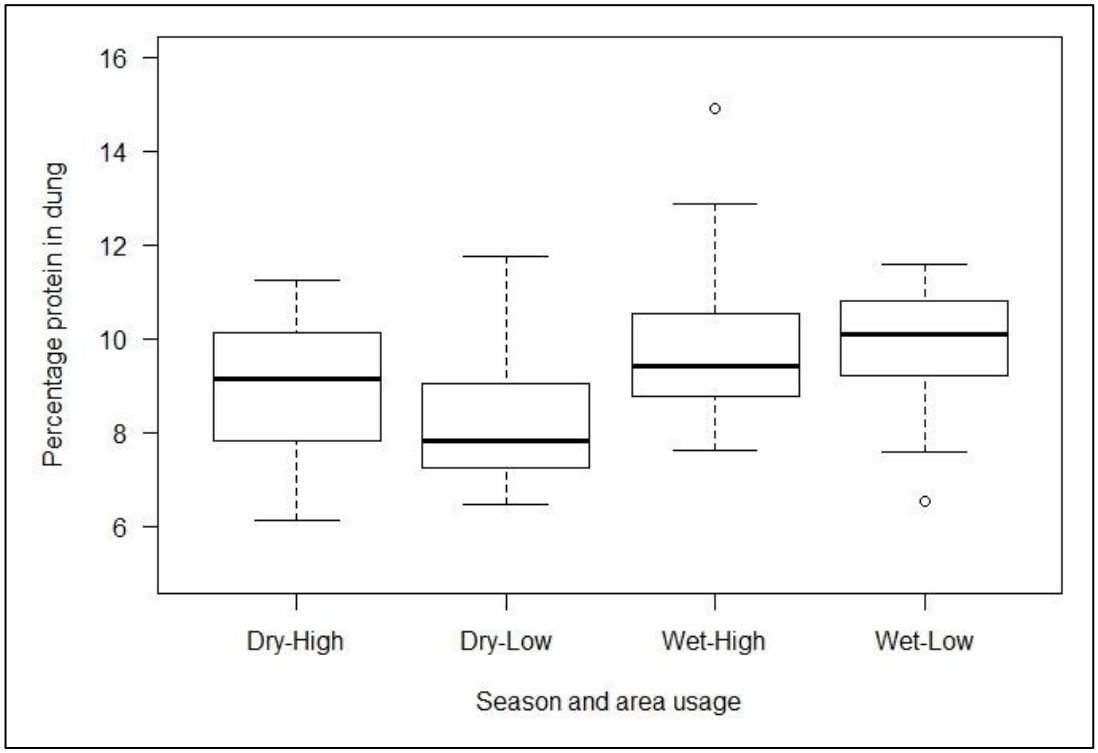

Fig. 4.5. *Crude protein content (%) of wildebeest dung for season and region. No significant differences between season and region were observed.*

4.3.5 Herbivore grass species preference

My analysis of grass species selection patterns by the KTP grazer community show that grass species use is not in proportion to grass species abundance in either the wet ($\chi 2 = 718.33$, df = 8, $P < 0.001$) or dry season ($\chi 2 = 892.42$, df = 7, $P < 0.001$). Post hoc chi-square tests reveal many significant differences between species when performing a series of pairwise comparisons, which suggests that grazers show clear preference among individual grass species (Fig. 4.6). However, grazers appear to be more selective during the wet season, on account of the higher number of significant differences between grass species pairs in the wet season compared to the dry season. *Eragrostis porosa* was the least preferred species in both the wet and dry season, while *Panicum coloratum*, *Stipagrostis obtusa* and *Enneapogon desvuaxii* were among the most preferred species year round. Overall, a greater percentage of grasses were recorded as being grazed during the dry season (79.3%) than during the wet season (54.8%).

Spearman rank correlations between my grass species preference index and measures of forage quality were not significant in the wet or dry season for either grass C:N ratios (wet: rho = 0.262, P = 0.54; dry: rho = -0.643, p = 0.14) or crude protein content (wet: rho =-0.353 , p = 0.40; dry: rho = 0.071, p = 0.07; Fig. 4.7). Although not significant at the 95% confidence level, note that the relationship between the species preference index and crude protein content in the dry season was marginally significant, providing weak evidence that grazer preferences for different grass species may be related to forage quality in the dry season.

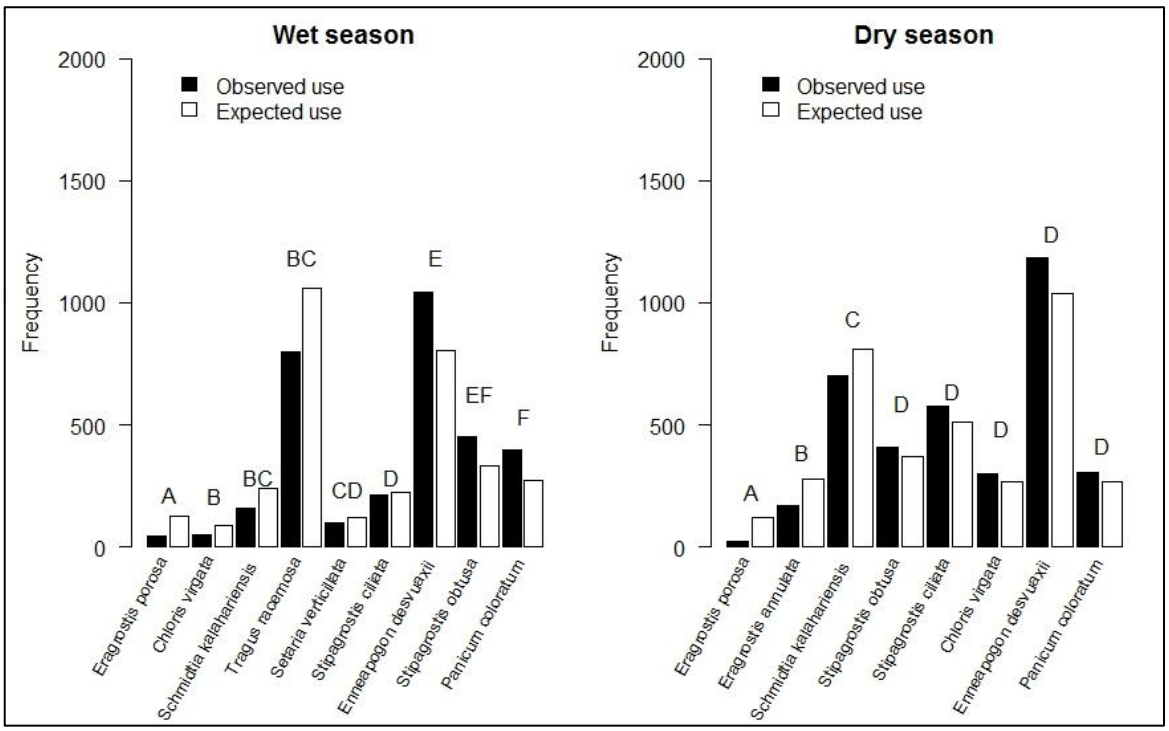

Fig. 4.6. *Chi-squared results comparing observed vs. expected grass species usage (based on availability) for the wet and dry season respectively. Y-axis values are frequency counts of each grass species. Species sharing the same letter do not differ at the 95% confidence level.*

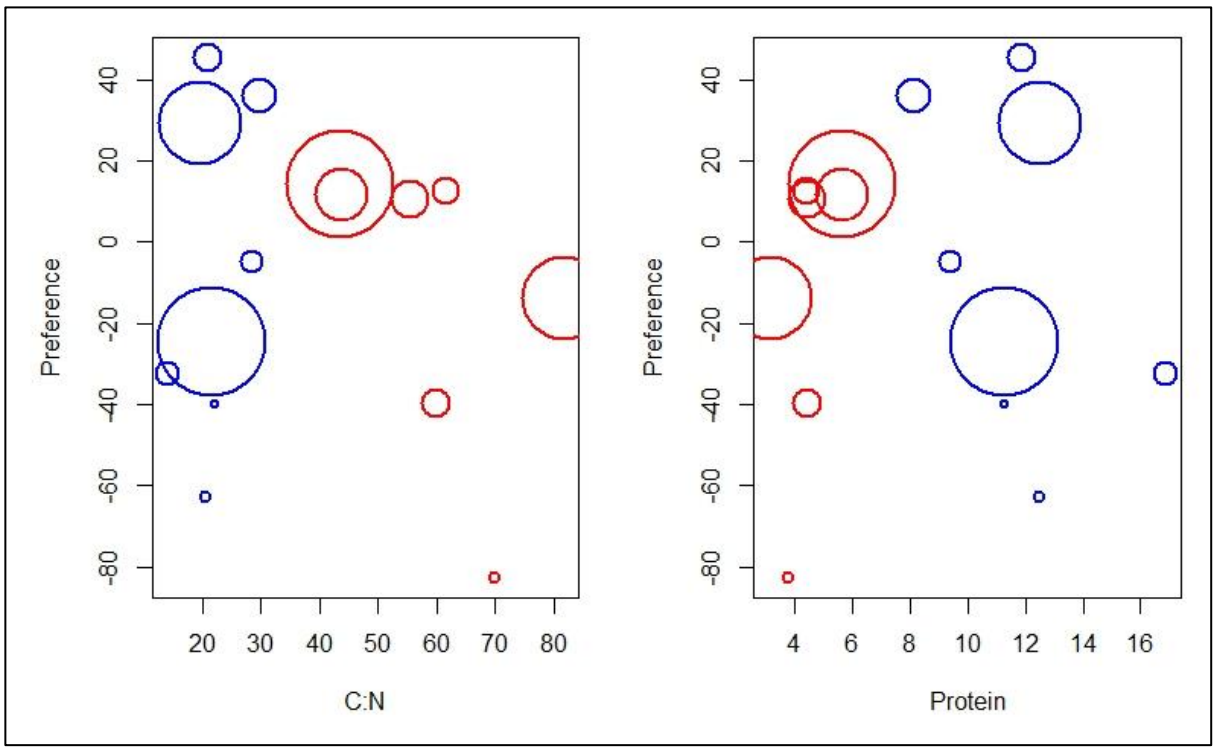

Fig. 4.7. *Relationship between grass species preference index and forage quality (C:N ratio and crude protein). Blue circles represent the wet season and red circles represent the dry season. Point size determined by abundance of species.*

4.4 Discussion

There is a strong relationship between regional wildebeest abundance and grass quality in the dry riverbeds of the KTP. My results show that regions of the riverbed that are favoured by wildebeest have significantly higher forage quality than those areas in which wildebeest are scarce. The distribution of savannah herbivores is largely governed by forage quality, influencing animal movement over many scales from local habitat selection (e.g. Bjorneraas *et al.* 2012) to large scale migrations (Senft et al. 1987; Williamson et al. 1988; Fryxell 1995). Forage heterogeneity is therefore expected to be a key determinant in the distribution of wildebeest in the KTP, particularly given the spatial and temporal patchiness of rainfall-driven grazing resources (Knight 1990; Verlinden & Masego 1997).

My results show that forage quality was significantly higher in the wet season compared to the dry season in both high and low use areas. Dry season forage quality did not differ between areas of high and low wildebeest abundance. This shows that, similar to the findings of other studies of Kalahari wildebeest (Selebatso *et al.* 2017) and contrary to herbivore

habitat selection in other areas (e.g. Said *et al.* 2009), the distribution of wildebeest at my study site is not governed by dry season forage quality. Forage quality does however differ significantly between high and low use areas in the wet season, with forage in high use areas showing elevated levels of crude protein. Wildebeest are therefore making more use of areas where the dominant grass species provide higher quality forage during the wet season. While wildebeest do not rely on fat reserves to see them through the dry season, wet season grazing is still important for these animals (Parker *et al.* 2009). Females also require high levels of protein during this time in order to meet the demands of giving birth and feeding young, and are likely to select for areas with higher forage quality if possible (Murray 1995; Voeten *et al.* 2010).

My results also show that the wildebeest in the KTP include a higher proportion of C_3 vegetation in their diet than recorded in other regions of their range (Van Zyl 1965; Skinner & Smithers 1990; Codron et al. 2005; Botha & Stock 2005) (overall 25% C_3 consumption). The high level of browse increases to almost 35% in more marginal, low use habitats during the dry season. The timing of this greater reliance on shrubs, forbs or other C_3 plants in the low use areas corresponds to variations in forage quality, with the average crude protein content of the dominant grass species in these areas dropping well below the 7-8% minimum (Beekman & Prins 1989) during the dry season. In contrast, wildebeest C_3 consumption remains relatively low in high use areas during the wet season when forage quality is higher. Despite the seasonal and regional fluctuations in grass quality wildebeest were able to maintain dietary crude protein levels above the 7-8% maintenance threshold level (Beekman & Prins 1989), even when dry season forage quality dropped well below 8%. The overall high levels of crude protein observed in wildebeest diet suggest they are managing to preferentially select higher quality components of the available forage during the dry season. This suggestion has weak support from the observed relationship between grass selection preferences of the wider grazer community, and crude protein content of the dominant grass species, particularly during the dry season when this relationship is marginally significant. Although this pattern reflects the grazing choices of all herbivores in the KTP, wildebeest make up a large portion of the grazer community and this pattern is therefore likely to broadly reflect the foraging patterns of wildebeest.

This emphasizes the dietary adaptability of these large ruminants and demonstrates their ability to incorporate more C_3 plants into their diets. While it cannot be assumed that the C_3

component of wildebeest diet consists of C_3 browse, the results of this study suggest that the low $\delta^{13}C$ values evident in wildebeest diet do not reflect C_3 grass consumption. The mean $\delta^{13}C$ values of all grass samples for my study is -13.0‰ (ten species, n = 120) which is a very strongly C_4 signal. Also, no study in southern Africa has found any C_3 grasses in warm season rainfall areas such as at my study site (Ellis et al 1978, Vogel et al 1978, February & Higgins, 2010). This suggests that these animals are consuming relatively high proportions of browse. Wildebeest in the South African section of the KTP do consume small amounts of forbs, showing selection for *Citrullus lanatus* as a means of obtaining water as well as grazing on green runners of the same species (Child *et al*. 1971; Knight 1991). During my fieldwork I witnessed wildebeest browsing on *Monechma incanum*, a small shrub found in abundance along the river banks. Another shrub, *Monechma genistifolium* subs. *austral* was similarly common, and both showed evidence of extensive browsing. It is therefore likely that perennial shrubs such as *Monechma sp.*, as well as some species of forbs, are important components of wildebeest diet, especially in marginal habitats during the drier months of the year. As a result, an alternative hypothesis for the observed relationship between crude protein content and grass species selection of the wider grazer community during the dry season is that the C_3 component of wildebeest diet may play a vital role in maintaining their crude protein intake. This emphasises the need for further research on the C_3 component of wildebeest diet in the KTP.

The extent to which this switch to C_3 browse would satisfy their nutritional needs remains unknown, as the effectiveness of grazing species in dealing with secondary compounds associated with ingested browse is poorly understood (Gordon 2003). For example, some grazing species lack the alimentary tract microflora present in the stomachs of browsers that aid in the digestion of browse materials (Jones *et al*. 2001). Wildebeest that become relegated to more marginal habitats where they are forced to incorporate very high levels of C_3 plants may thus become most susceptible to rapid declines in body condition. However, given the observed levels of crude protein in wildebeest diet, there is no current evidence that this is the case.

Although this study suggests that the broader grazer community selects for better quality forage in the dry season, there is no evidence to suggest that this preference takes place in the wet season. This is perhaps unsurprising from a crude protein perspective as the majority of dominant grass species in the wet season have crude protein content above the required levels

for large grazers. The observed selectivity for certain grass species in the wet season is therefore likely to be governed by other factors such as grass height and palatability, which would influence feeding rates for herbivores. Optimal foraging theory, simply states that an animal will use the minimal amount of time and energy to acquire the optimum amount of food resource s (Belovsky 1997). This theory may explain the observed selectivity and trade-offs wildebeest confront when searching for food in the riverbeds of the KTP.

CHAPTER 5

Synthesis

Although the provision of waterholes has facilitated the formation of a largely sedentary population of wildebeest in the KTP, the effects of environmental variables such as the quality of water as well as the abundance of forage, tree density and river width also contribute to wildebeest habitat selection. Water quality emerged as a key predictor of wildebeest presence. Areas with access to fresh water strongly influences wildebeest distribution, so much so that areas with saline water are of similar importance to wildebeest as areas with no water.

The abundance of wildebeest in the riverbeds of the park does change seasonally, with animals moving out of the riverbeds during the wet season when forage quality improves. This local movement does not contrast with the historical movement of wildebeest in this area, that were recorded moving into the broader KTP during the wet season, presumably to utilize the increased forage during this time. My results would suggest however, that the wildebeest are returning to the riverbeds during the drier months of the year instead of following the historical routes north-east back into the Kalahari (Eloff 1961; Child *et al*. 1971; Williamson *et al*. 1988; Mills & Retief 1984).This dry season concentration in the riverbeds is almost certainly a result of the provision of surface water in these areas, particularly fresh water which these animals have become reliant upon during the dry season.

In this semi -arid system access to shade (or the density of shade-providing trees) also plays a role in shaping wildebeest distribution. This demonstrates the importance of thermoregulatory behavioural adaptations in these arid ecosystems - wildebeest are likely attracted to areas with more shade to escape the intense heat, particularly during inactive periods when they are ruminating (Ben-Shahar & Fairall 1987). Wildebeest were also shown to avoid areas with dense vegetation and select for sections of the riverbed that are wide and open. Open areas devoid of cover decrease the risk of predation (Riginos & Grace 2008; van Rooyen *et al*. 2008), and also offer wildebeest with a larger area of their preferred short grass habitat and, as a result, increased forage. Forage availability is a key determinant of herbivore distribution, and this study provides strong evidence for the important role of forage abundance in wildebeest habitat selection in the riverbeds of the KTP. Forage quality also determines wildebeest distribution in the Park, with areas with higher quality forage showing

higher densities of wildebeest during the wet season, while areas of low wildebeest abundance also had low forage quality.

A more detailed investigation into the feeding ecology of wildebeest reveals that the animals in this system consume a high amount of C_3 plants in comparison to other areas of their distribution. The C_3 component of the diet was particularly high in marginal, low use areas in the dry season, indicating that C_3 plant consumption in this system may be of particular importance to these animals during periods of drought. Interestingly, my results show that wildebeest were able to maintain their crude protein requirements throughout the dry season, even though my data collection took place during a particularly dry period over the last 30 years. This suggests that these animals are currently not food limited. Wildebeest abundance in the riverbeds still appears to be largely governed by bottom up (resource-based) as opposed to top-down (predation-based) mechanisms. Nonetheless, predators may play an indirect role in influencing wildebeest habitat selection through the landscape of fear, as wildebeest show greater use of areas where predation risk is perceived to be lower. Further research into the C_3 component of wildebeest diet, as well as further investigation into the role predators play in regulating the wildebeest population, are necessary.

While several studies have shown that water provision has influenced the wildebeest population in the KTP (Mills & Retie 1984; Mills & Retief 1984b), the consequences of this behavioural shift on vegetation structure are not known. The natural vegetation structure between high and low use regions differs considerably, making it hard to ascertain the long term impacts of a sedentary wildebeest population on vegetation in specific areas. Given that the provision of permanent surface water began over 80 years ago, it is likely that plant communities have already been affected. It may be possible to restore the historical grazing regime previously experienced in the region by closing a portion of the waterholes in certain seasons – restricting access to fresh water holes in the dry season would force wildebeest to utilize these areas in the wet season only. This would likely shift the grazing regime in areas around these water holes to reflect the historical pattern of wet season use and dry season absence experienced in the past. However, it is important to consider the impact this may have on the resident population, who have had access to surface water throughout the year for a substantial period of time. It would therefore be vital for management to further investigate this suggestion before implementation, especially considering the important tourism and conservation objectives of the park as a whole.

Supplementary Information

Table S3.1. *Multiple R-squared values for all pairs of predictor variables included in additive models of landscape use by wildebeest.*

NDVI	0.001			
Water	0.034	< 0.001		
Temperature	< 0.001	0.001	< 0.001	
River width	0.008	0.002	0.097	< 0.001
	Trees	NDVI	Water	Temperature

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